INSECT PHYSIOLOGY

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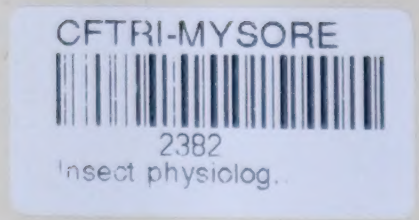

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To the insect, order and disorder are exposed to sight;
and so we think to see the little emmets confer
and locking their antennae immediatly transmit
the instinctiv calls which each and all can feel; whereas
the mutual fellowship of distributed cells
hath so confounded thought that explanation is fetch'd
from chemic agency: because in that science
the reaction of unknown forces is described and summ'd
in mathematic formulae pregnant of truth,
and of such universal scope that, being call'd laws,
their mere description passeth for Efficient Cause.

—ROBERT BRIDGES

INTRODUCTION

THE fundamental processes of vital activity, the ordered series of physical and chemical anges which liberate energy and maintain the nmanent movement' of life, are probably the me wherever 'living matter' exists. The scription of these changes is the ultimate goal physiology, of whatever group of organisms; t the tissues of insects have been so little idied from that point of view, that in this ok we shall be concerned only with physiology a humbler plane: with the grosser functions the organs and tissues, and with the mecha-sms by which these functions are co-ordinated serve the purpose of the insect as a whole.

Of all the zoological classes, the insects are the ost numerous in species and the most varied structure; the general physiology of the group therefore only too apt to be obscured by the dless specializations of particular forms; and

the main difficulty of a work like the present is the exclusion of all that is special and non-essential, and the retention of only that material which best illustrates the general theme. There are, indeed, certain common factors which condition the physiological make-up of the insects, and these factors serve, to some extent, to link them all together into one system. They are essentially terrestrial animals. This circumstance determines the characters of their cuticle, and this, in turn, conditions their respiratory mechanism and the physiology of their growth. The respiratory mechanism and the cuticular skeleton are among the factors which restrict the size of insects. Their small size and terrestrial habit render them very prone to lose water; and the urgent need for the conservation of water influences the respiratory, excretory and digestive systems. All these systems show special changes when the insect reverts to an aquatic life.

Yet, although the interaction of these factors results in some uniformity of principle in the physiology of insects, their diversity in habit, food and environment causes such endless variation in detail, that, quite apart from the conspicuous gaps in our present knowledge, any limited treatment of the subject must in any case be more or less arbitrary in presentation; and, were there space to insert them, nearly all the generalizations that are attempted should have qualifying instances.

The history of insect physiology is peculiar. The early microscopists, Hooke, Malpighi, Leeuwenhoek, made many observations on the structure of insects, and many accurate inferences

about their physiology. More was added by the great naturalists, Swammerdam, Réaumur, de Geer. But, with such conspicuous exceptions as Newport, Graber, Lubbock, Plateau, and others of more modern times, the majority of entomologists, until recent years, have been so fully occupied with the morphology and taxonomy of their colossal group that such advances in physiology as have been made have commonly been mere by-products of morphological study. From time to time we find the physiologists of the last century, Dutrochet, Treviranus, Marshall Hall, v. Kölliker, Claude Bernard, turning to the insects to illuminate their theme; but their concern was not with the insect as such.

Within recent years, interest in the physiology of insects has arisen in a new quarter. The applied entomologist, confronted with the ravages of insects in the spheres of agriculture and of public health, has wanted to know something about their nutrition, about the laws governing their responses to sensory stimuli, about their reactions to parasites, about the precise way in which their bodies are adapted to diverse climatic conditions, and about the action upon them of toxic sprays and gases. With this demand for increased knowledge has come a realization of our present ignorance.

The sketch which follows is based on the study of nearly 2,000 publications, and on a certain amount of original work. It has not been possible to include references to all these sources; some 300, only, have been selected—most of them recent works which will introduce the student to the earlier literature. For this reason, reference

to a given author is not intended to imply that this author was necessarily the first to have made the observations in question; many such references are to textbooks and reviews.

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INSECT PHYSIOLOGY

CHAPTER I

THE INTEGUMENT

THE key to much of the physiology of insects is to be found in the nature of their cuticle. As was first shown by Haeckel, the cuticle consists of non-living material, the product of a living matrix —a single layer of epidermal cells. Its most familiar constituent is the nitrogenous polysaccharide—chitin ; but neither qualitatively nor, in some cases, even quantitatively, can chitin be considered its most important element. For chitin rarely makes up more than 50 per cent. of the cuticle ; more often it forms only about 30 per cent. [53, 152] ; and the most characteristic properties of the cuticle, its rigidity and its impermeability, are not dependent on the chitin present. For those parts which are richest in chitin, the inner layers, are the most flexible and elastic ; and where chitin is present without the other constituents, as in the anal papillae of mosquito larvae (p. 68) or in the peritrophic membrane of the intestine (p. 46), the structure is freely permeable to water and to many substances in solution.

Composition of the Cuticle. The cuticle is indeed a very complex tissue. It consists of two primary layers : a relatively thick *endocuticle*, known also as the ' Hauptlage ' or ' Innenlage ', composed of chitin and of an insoluble protein ; and a very thin *epicuticle* or ' Grenzlamelle ' [168]. This latter

contains neither protein nor chitin ; it is only about 1μ in thickness ; yet it appears to confer upon the insect cuticle its essential property of impermeability. For the substance of this epicuticle the name 'cuticulin' has been proposed [286]. It bears much the same relation to the underlying chitin layer as the delicate cuticle of the plant does to cellulose. Chemically, also, it seems closely allied to the plant cuticle, resisting solution in concentrated sulphuric or hydrochloric acids, in which the endocuticle dissolves, but dissolving in caustic alkalies, to which chitin is resistant. It is not a protein nor a carbohydrate nor a simple fat ; perhaps it is a complex mixture of combined fats or waxes [168]. It is evident that the biological importance of this remarkable substance makes it a most desirable subject for chemical study.

The protein of the endocuticle is readily demonstrated by the protein colour tests : the biuret, Millon's and xanthoproteic reactions, all of which are intensely positive [286]. The best test for chitin is that of van Wisselingh, which consists in its conversion into chitosan by strong caustic potash at a high temperature, and the recognition of chitosan by its solubility in acids and by the violet colour it gives with iodine [53]. The cuticulin of the epicuticle is a less well-defined substance ; quite likely it is a mixture ; its most characteristic properties are its insolubility in strong mineral acids, and its rapid fusion into oily droplets when heated in the presence of caustic potash and potassium chlorate (cerinic acid test) [168].

In unstained sections, the endocuticle is colourless, the epicuticle typically amber-coloured. But in many parts, where the cuticle is rigid and inflexible or 'sclerotized', the outer part of the endocuticle, also, is impregnated with the amber-coloured cuticulin, often more or less mixed with melanin ; and thus a third layer is formed in which chitin, protein, 'cuticulin' and other substances are present. This

layer is responsible for the rigidity of the cuticle; it is variously termed the *exocuticle*, 'Emailschicht' or 'Lackschicht' [286].

In a few insects the cuticle contains lime. Sometimes this forms a superficial deposit on the spines of aquatic larvae (*Pericoma*, Psychodidae, Dipt.) from waters rich in calcium bicarbonate [165]; some-

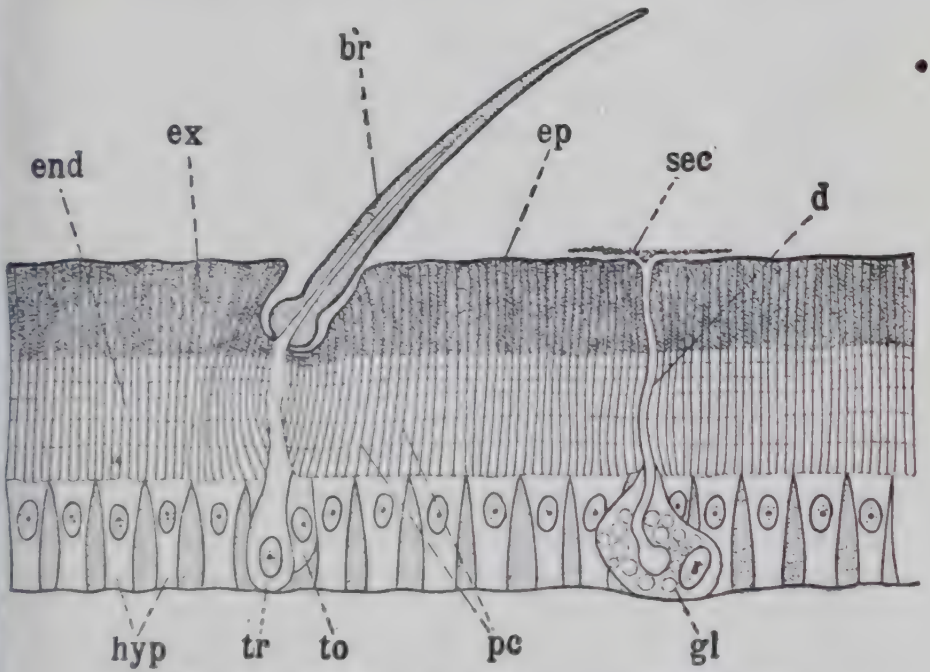

FIG. 1.—The insect cuticle: semischematic

br, hair or bristle; *d*, duct of dermal gland; *end*, endocuticle; *ep*, epicuticle; *ex*, exocuticle; *gl*, dermal gland; *hyp*, epidermis (hypodermis); *pc*, pore canals; *sec*, "Sekretschicht"; *to*, tormogen or socket-forming cell; *tr*, trichogen or hair-forming cell.

times it is laid down, before moulting, in pits in the new cuticle called calcareous warts (Stratiomyidae, Dipt.) [198].

Finally, there is sometimes a layer which is believed to be formed by the outpouring of secretion from the dermal glands at the time of moulting. This is termed the 'Sekretschicht'. It is not always present, and sometimes it amounts to nothing more than a

little dried secretion of no functional significance [286]; but sometimes it is an important layer; and in the case of many of the brilliantly coloured Cicindelidae, it is apparently the layer which is responsible for the metallic tints [240]. Its chemical nature is unknown.

Structure of the Cuticle. The histological structure of the cuticle is no less complex than its chemistry. It is most commonly described from stained sections, and in these the epicuticle and exocuticle, which do not stain, appear homogeneous and structureless; the endocuticle shows more or less conspicuous horizontal lamellae. In some preparations the endocuticle shows also very faint vertical striations—the so-called 'pore-canals'. The older histologists paid considerable attention to these structures; but in sections prepared by modern histological methods they are so inconspicuous that most recent authors have neglected them, regarding them simply as processes (pseudopores) from the epidermal cells, which have become chitinized. But if the cuticle of certain insects (*Rhodnius*, Hem. [286], *Tenebrio* larva, Col. [288], *Periplaneta*, Orth. [288]) is cut in the fresh state with the freezing microtome and mounted without staining, the pore-canals are very conspicuous objects (often far more conspicuous than the horizontal lamellae) running right through the endo- and exocuticle, though not piercing the epicuticle (Fig. 1). Moreover, the canals are patent, and contain protoplasmic processes or fluid; for if the sections are allowed to dry in the air before being mounted, the canals become filled with fine threads of gas. The cuticle is therefore not entirely dead; like the bone and dentine of vertebrates, it probably contains cytoplasmic filaments.

In the past there has been a certain amount of controversy as to whether, microscopically, the substance of the endocuticle has a foam-like structure or a fibrillar structure [168]. At the present time one would probably be safe in dismissing both these views

and regarding this substance as an elastic gel, which in many insects is formed around protoplasmic filaments from the epidermal cells (the pore-canals), and in nearly all cases is, by some unknown mechanism, laid down in a succession of lamellae. The extent to which the endocuticle can be stretched, when it is not impregnated with cuticulin, is often astonishing: the first stage larva of *Rhodnius* can receive into its abdomen more than twelve times its own weight of blood. The epicuticle, on the other hand, apparently cannot be stretched; it is often highly convoluted, and it accommodates itself to changes in volume by the smoothing out of the folds in its surface [286].

A rather special arrangement of the endocuticle is met with in the rigid armour of beetles. Here each layer of the endocuticle is made up of a series of parallel rodlets (' Balkenlagen ') with interstitial substance of a different nature between them. The ' Balken ' of each successive layer are set at an angle to those above and below; an arrangement which probably increases the inflexibility of the cuticle. In these cases the pore-canals run upwards between the criss-crossing ' Balken ', appearing in surface view as stellate points [240, 238].

Surface Forces and the Insect Cuticle. Since the surface of a body varies with the square of its radius, whereas its volume or mass varies with the cube of its radius, it follows that the ratio of surface to mass becomes progressively greater as the size of the body diminishes. Consequently, the forces resident in surfaces become relatively stronger. In the case of insects, the surface forces are, indeed, frequently great enough to move the whole mass of the body; and they introduce a factor into the life of insects, particularly when they come into contact with water, which is unnoticed by larger animals. It is necessary, therefore, to consider the properties of the cuticle from this point of view.

As a general rule, the cuticle is not readily wetted by water ; there is, in fact, a large ' angle of contact ' between the water surface and the cuticle (Fig. 2, A) [37]. Consequently, when an insect stands on water, the surface tension acts in the opposite direction to gravity, and the insect is held up as though by an elastic membrane. This ' hydrophobe ' property may belong to the epicuticle ; but in some cases at least it is accentuated by the presence of glands

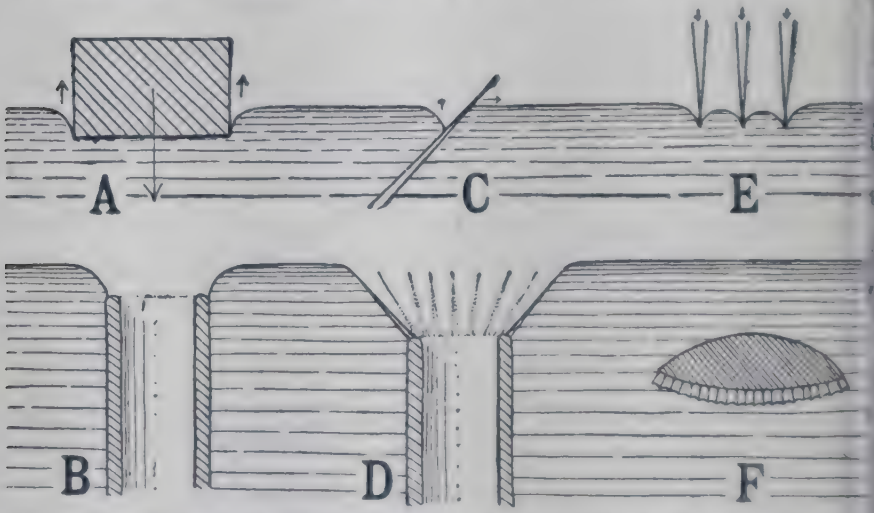

Fig. 2.—Diagrams illustrating the properties of the insect cuticle in contact with water

A, hydrophobe object supported by the surface tension of water ; B, respiratory siphon with hydrophobe rim similarly supported ; C, surface forces acting on a hydrophobe hair brought obliquely to the water surface ; D, a crown of such hairs supporting a respiratory siphon ; E, hydrophobe hairs brought vertically against the water surface ; F, insect body with a ventral covering of such hairs carrying a layer of air.

producing a fatty secretion [24]. That is the case, for example, around the spiracles of Muscid larvae, and around the respiratory tube of the larva of *Eristalis*, by means of which this insect, like many other aquatic larvae, is enabled to hang suspended from the surface film with the remainder of its body submerged (Fig. 2, B) [282].

The effect of surface forces becomes still more evident when hairs or bristles are present on the body.

Where a fine pile of these hydrophobe hairs is set vertically on the body surface, they hold the water at a distance, so that the insect, when it goes below the water surface, can carry with it a film of air (Fig. 2, E, F). We shall see that this film has some remarkable properties in relation to the respiration of aquatic forms (p. 29). Then, if a single bristle is inclined at an angle—for simplicity we will suppose at an angle of 45°, and we will suppose that the angle of contact is also 45°—and brought up to the water surface from below, as can be seen from Fig. 2, C, the surface tension of the water will draw it over so as to increase the angle of inclination. It will behave as though the one surface were hydrophile and the other hydrophobe. Many insects hold themselves at the water surface for purposes of respiration by means of rows or circles of such bristles (Fig. 2, D) [37].

Terrestrial insects avail themselves of surface forces in quite a different way: namely, in order to cling to surfaces too smooth to provide a purchase for their claws. The physical mechanism of the organs (pulvilli and such like) that are used for this purpose is by no means certain in all cases; but in one example that has been recently studied (that of the bug *Rhodnius*) [289], it has been shown that the insect is held by the adhesion or seizure of the climbing organ to the surface. In other words, it is the surface molecular forces that are directly concerned in supporting the body weight.

The Moulting, Formation and Pigmentation of the Cuticle. Through the possession of a more or less rigid carapace, incapable of increasing its surface area once it has been laid down, the insect incurs the necessity for discontinuous growth. In later pages (p. 89) we shall consider some of the physiological processes which lie at the back of insect growth; but one change which it always involves is the casting of the old cuticle, and the formation of a new and larger one. This side of growth, or

ecdysis, may be conveniently considered here, for it throws a good deal of light upon the properties of the insect cuticle.

Chitin is a nitrogenous substance, though its nitrogen content is relatively small (about 8 per cent. —only half that of protein), and the suggestion has therefore frequently been made that it is really a waste product, and moulting or ecdysis an excretory phenomenon. But this idea fails to take into account the fact, which has long been known, that during moulting most of the old cuticle is dissolved, and is not, in fact, lost to the insect. In a recent study of moulting in the bug *Rhodnius*, it has been shown that only about 14 per cent. of the cuticle of the abdomen is actually shed; the remaining 86 per cent. is re-absorbed by the insect and is presumably used again for the formation of the new cuticle [286].

This process of digestion and absorption of the cuticle raises many interesting problems in physiology. (i) Firstly, what is dissolved? Only the endocuticle is dissolved, the chitinous and protein layer; the epicuticle is quite untouched; and when the outer part of the endocuticle is impregnated with cuticulin (that is, when an exocuticle is present) this also is quite untouched [286]. (ii) Secondly, how is solution brought about? Between the old cuticle and the new is a thin layer of fluid, the exuvial or moulting fluid; this must be responsible for dissolving the cuticle. Now the moulting fluid is a more or less neutral fluid incapable of attacking the chitin and scleroprotein of the cuticle by simple chemical action; and it contains no cellular elements. It must therefore contain digestive enzymes: a chitinase and a protease [286]. (iii) Thirdly, where do these enzymes come from? Those insects in which the digestion of the endocuticle is most marked, the Lepidoptera [263], the Coleoptera [211], the Hemiptera [286], possess well-developed dermal glands which become active at the time of moulting; and, at any rate in the case of

the bug *Rhodnius*, the onset of functional activity in these glands coincides with the commencement of digestion of the old cuticle [286]. It is therefore highly probable that they are responsible for the production of the enzymes in the moulting fluid ; although, of course, this does not exclude the possibility that much of the fluid itself may be exuded by the general epidermis [139]. (Later (pp. 60, 90) we shall have to consider other hypotheses as to the function of these glands.) (iv) Fourthly, by what route are the products of digestion absorbed ? Now the quantity of moulting fluid present at any moment is very small ; it often amounts to little more than a moist film, far thinner than the old endocuticle that is to be dissolved (Fig. 3, A). It is clear, therefore, that the moulting fluid must be circulating and carrying with it into the body of the insect the products of digestion. At the time of moulting in the silkworm, much of this fluid is swallowed by the mouth [265], but in *Rhodnius*, the only other insect in which this problem has been considered, the absorption seems to take place through the general surface of the newly-formed cuticle [286].

This raises the question of the resistance of the new cuticle to solution by the moulting fluid, its method of formation, and its permeability. (i) The new cuticle resists digestion presumably because the non-chitinous epicuticle is secreted first ; the protein and chitin of the endocuticle are therefore protected from the enzymes in the moulting fluid [286]. (ii) The method of formation of the endocuticle probably varies in different insects, and according to the structures that are to be formed. Sometimes, as in the developing bristles, a cellular process gradually becomes impregnated with chitin and cuticulin : these secretions are laid down intracellularly. Often, the material of the endocuticle seems to be separated in fluid or semi-fluid form around the filamentous processes from the epidermal cells, which later constitute the pore-

canals [209] [286] : it is only a question of words whether this phenomenon is called cellular transformation or secretion. (iii) The permeability of the cuticle when newly formed must be very different from its per-

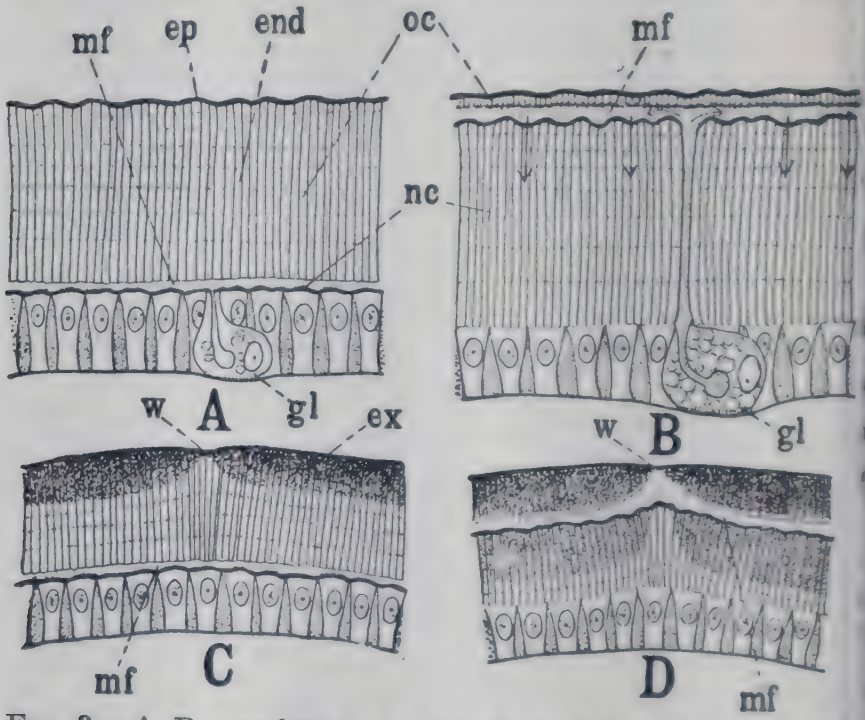

FIG. 3.—A, B, moulting of a cuticle in which an exocuticle is wanting. (Modified after Wigglesworth.) In A the new epicuticle is formed; the digestion of old endocuticle has scarcely begun. In B the digestion and absorption of the old endocuticle is almost complete. C, D, transverse sections through the prothorax of an insect at stages corresponding with A and B, showing the absence of exocuticle at the line of weakness. (Semischematic.)

end, endocuticle; *ep*, epicuticle; *ex*, exocuticle; *gl*, moulting gland; *mf*, moulting fluid; *nc*, new cuticle; *oc*, old cuticle; *w*, line of weakness in cuticle.

meability when mature. For we have seen that the mature epicuticle is impermeable to water; but if the foregoing account is correct, up to the time when the old skin is cast, it must remain freely permeable both to water and to the digestion products of the

endocuticle. In other words, at the time of moulting some essential change takes place in the properties of the epicuticle.

Up to the time of moulting the new cuticle is soft and almost colourless. Within an hour or two of the casting of the old skin, it has both hardened and darkened ; and it is probably during this process that its impermeability develops. The two processes of melanin formation and the hardening of the cuticulin take place at the same time ; but they are separate processes, because the dark areas are not necessarily harder than the pale [121]. Now the formation of melanin is known to be dependent upon the access of oxygen ; it is natural to suppose that the hardening of the cuticle is equally so ; and the obvious conclusion is that the shedding of the old skin exposes the new skin to the air and both hardening and blackening can then proceed.

But it is more complicated than that. For if the new cuticle is exposed to the air by dissecting away a portion of the old cuticle twenty-four or forty-eight hours before the insect is due to moult, although the epicuticle is at this time fully formed, darkening and hardening do not take place until the insect is ripe for moulting one or two days later [286]. And conversely, insects which have failed to moult for various reasons, may have their new cuticle perfectly hardened and pigmented beneath the remnants of the old skin. In other words, the influence which brings about these changes is exerted from *within* the insect, presumably by the epidermal cells. Not uncommonly, the changes in question are confined to the epicuticle ; so that the epidermal cells must exert their influence through the substance of the endocuticle, which is itself unaffected. (It is true that in many cases the bulk of the endocuticle is laid down after moulting [238], and when this is so the epidermal cells are in direct contact with the ' Pigmentschicht ' during the process of darkening.) Perhaps we have here the function

of the pore-canals: they enable the epidermal cells to effect, from a distance, oxidative enzymic changes in the epicuticle [66, 286]. As we shall see later (p. 82) it is probably the oxidizing enzyme which is conveyed by the pore-canals; the substrate or chromogen being previously localized in the cuticle and so determining the distribution of the pigmentation [107].

The Mechanism of Moulting and of Hatching. When the insect has digested its old cuticle and laid down the new one, it has fresh problems to solve. In the first place, it has to rupture the old skin and escape from it. Now any cuticle that has to be shed, that is, the cuticle in every stage except the adult, has a 'line of weakness'—sometimes in the head, most often in the mid-line of the thorax [80]. Along this line the exocuticle is wanting, and the endocuticle extends right up to the very delicate epicuticle (Fig. 3, C). Consequently, when the endocuticle is completely dissolved (and the process of moulting is so timed that this happens just when the new cuticle is ready) the old skin needs but the slightest force for it to split along the line of weakness (Fig. 3, D).

The rupturing force is the pressure of the blood. The insect contracts the abdominal muscles, often repeatedly in a peristaltic fashion, and so increases the pressure of blood in the thorax, which bulges outwards until the old skin splits. Many insects add to the efficiency of this process by first swallowing air [38] (as vertebrates fill the lungs with air during defaecation or parturition) or, if they are aquatic, by swallowing water [25]. Once the old skin is split, the insect escapes from it by gentle peristaltic movements, often aided by gravity—for many insects hang head downwards during moulting [80].

It is commonly stated that the moulting fluid serves as a lubricant to facilitate this process—indeed, that is often considered to be its chief function. But in many insects the moulting fluid has practically

disappeared by this stage; the insect is quite dry, the inner surface of the old skin only slightly moist [286]; and in many aquatic and terrestrial pupae a layer of air appears before hatching between the pupal skin and the developed adult—due, no doubt, to the energetic absorption of the moulting fluid.

When the insect has withdrawn its limbs, and freed itself completely from the old skin or from the pupa, it must enlarge the new cuticle rapidly to the required size, and bring about the expansion of its wings, before the epicuticle has hardened. This it does in the same manner, by swallowing more air or water, and forcing the body fluid under pressure into the wings. In the Ephemeroptera and in many Lepidoptera the sole function of the gut in the adult insect is to receive air for this purpose. If the crop of the cockroach is pricked with a needle, the distension of the new cuticle cannot take place, and the insect collapses like a pricked balloon [80]; or if the tips of the wings in the dragon-fly are cut off, blood drips from them and they cannot expand [38].

We may note here that the process of hatching from the egg is similar in many particulars to that of moulting or emergence from the pupa. It is not known whether the amniotic fluid in which the embryo is bathed contains digestive enzymes which weaken the membranes of the egg, nor whether any of this fluid is absorbed through the general surface of the young insect's skin; but in many cases the fluid is swallowed by the mouth shortly before hatching [290] (like the moulting fluid of the silkworm). Many insects then tear or bite their way out of the egg. Others swallow air, and by muscular contraction of the abdomen, drive the head or thorax against the shell and cause it to burst open. Certain groups have special structures, spines, saws, hard plates or distensible bladders, which enable them to increase the efficiency of this process by concentrating the impact at one point of the egg, and so piercing the shell or

forcing off the egg cap [83, 290]. (This last arrangement finds a parallel in the ptilinum of emergent Muscid flies, which they distend with blood in order to force off the cap of the 'puparium' [80].) When the insect has left the egg, it commonly swallows air or water once more, and so increases its bulk before its cuticle has hardened [290].

Other Dermal Glands. Besides the glands which digest the old cuticle at the time of moulting (p. 8), and in some cases perhaps produce the 'Sekretschicht' (p. 3), and those concerned in the production of hydrophobe substances in the cuticle (p. 6), there are many other types of dermal glands in insects. Some of these are very like the moulting glands in structure; others are more complex multicellular glands; but they are nearly always lined with a delicate membrane continuous with the epicuticle [269]. These glands have the most varied functions. Sometimes, as in many Coccids, they produce a protective coating of wax, which may be moulded into beautiful forms as it passes through the orifices in the cuticle [268]. In the feet of Embioptera and Embiidae (Dipt.) they are silk glands. Sometimes, as in Lepidoptera, they are scent glands which occur only in the male sex, often discharging through specially modified scales on the wings and elsewhere; they are then generally credited with an aphrodisiac function [82]. Sometimes, as in Hemiptera and Blattidae, they are stink glands, producing a nauseous secretion which is held responsible for the immunity from predators which many such insects enjoy [149]. In certain beetles, notably Chrysomelidae, strongly smelling or bitter fluids may be ejected by dermal glands provided with large reservoirs [160]. In other insects fluids may be given out which produce urticarial reactions in the human skin.

This list by no means exhausts the multiplicity of dermal glands already known. But at the present time, the relation of these glands to the general phy-

siology of the insect is almost entirely unexplored. In some cases, as for instance in the larva of *Melasoma* (Chrysomelidae, Col.) in which the secretion contains the aromatic salicin concentrated from the willow leaves on which it feeds [259], it appears as though the insect has found a biological use for the waste products of its metabolism; but it cannot at present be claimed that that is so with the wax or other types of dermal glands.

CHAPTER II

RESPIRATION

TERRESTRIAL life is a perpetual conflict between the need for oxygen and the need for water; for those conditions which favour the entry of oxygen into the body, favour also the escape of water. This conception, applied to the insects, illuminates the whole subject of their respiration [115]. The majority of insects, as we have seen, have become encased in a waterproof covering; a covering which is relatively impermeable to oxygen also. They breathe, as was discovered by Malpighi, through tracheal tubes, which open along the sides of the body through a series of spiracles, and convey air directly to the tissues (Fig. 5, A). The tracheal trunks anastomose one with another, and then branch and rebranch, becoming finer and finer, until their ultimate ramifications either penetrate the individual fibres of the muscles or the cells of other tissues, or form a rich network over their surface [282].

The Tracheae and Tracheoles. Morphologically, the tracheae are invaginations of the ectoderm. Consequently, they consist of a cellular matrix and a lining cuticle. As the result, no doubt, of the physical stresses to which it is subjected during its formation, the cuticle is thrown into spiral folds, and sometimes, probably because the cells have continued to secrete the cuticular substance after the folds have developed, the final result appears as though the tracheae were made up of a uniform membrane, thickened with spiral filaments or taenidia [282]. This

spiral formation enables the tracheal tubes to be bent and pressed upon without collapsing.

The chemistry of the tracheal cuticle resembles that of the general surface of the insect. The innermost layer is composed of the non-chitinous 'cuticulin'; in the larger trunks a certain amount of chitin is present, presumably deeper to this [152]; but in the small branches chitin is absent [53]. Whether the substance of the finest branches is protein, or is related to 'cuticulin', is not known.

When the tracheal branches become reduced to about 1μ in thickness, they no longer show any spiral folding, and are then termed tracheoles or tracheal capillaries. Sometimes the transition from trachea to tracheole takes place gradually; but sometimes a tracheal branch of 2–5μ in diameter, after entering a large stellate 'tracheal cell', breaks up abruptly into a sheaf of fine tracheoles. On account of the readiness with which this tracheal cell stains with osmic acid, special properties have been attributed to it in connexion with respiration and tissue oxidations. But the evidence for these hypotheses is very slight; the tracheal cells are often absent; and altogether it is more probable that they are merely matrix cells of tracheae or tracheoles which have become spread out into a weblike form [282].

The permeability of the tracheal system shows a gradation from the spiracle to the tracheole ending. It is permeable to gases throughout [282]; though naturally it must be much more so where the walls become as delicate as they are in the tracheoles. Like the epidermal cuticle, it is probably impervious to water, except in the tracheoles which are freely permeable. Indeed, the terminal part of the tracheoles in many insects, both terrestrial [279] and aquatic [278], normally contains a variable amount of fluid (Fig. 4, A): and it is interesting to consider why this fluid does not extend up into the tracheae. For these tracheal capillaries are so small (about one-third or

less of 1μ in diameter) that, making certain assumptions, it can be calculated that the force of capillarity in them will approximate to a pressure of ten atmospheres. In other words, it will require a force of this magnitude to keep the fluid from rising in them. Whence can such a force be derived ? It probably comes from the osmotic pressure of the tissue fluids, which is in fact of this order of magnitude (p. 37). For if the tracheoles are exposed to salt solutions somewhat hypertonic to the insect's blood, more fluid is extracted from them, and the air extends

FIG. 4.—Tracheoles running to a muscle fibre : semi-schematic

A, muscle at rest ; terminal parts of tracheoles (shown dotted) contain fluid ; B, muscle fatigued ; air extends far into tracheoles. (Modified after Wigglesworth.)

downwards towards the tissues (Fig. 4, B). And if such solutions are replaced by hypotonic fluids, the air retreats again higher than before. These same changes can be brought about by the increase in osmotic pressure which accompanies muscular contraction ; so it is possible that these phenomena may on occasion have some physiological significance in improving the supply of oxygen to those tissues whose need is greatest [278]. It is probable that osmotic pressure is responsible also for the initial filling of the tracheal system when the insect hatches from the egg [290].

The lining of the larger tracheae is relatively hydrophobe (p. 6). Consequently, there is no tendency for water to enter the spiracles. And, of course, if the tracheoles on exposure to the air were also to become dry and hydrophobe, capillarity would be absent, and water from the tissues would not be drawn along them. Perhaps that is the case in those insects in which the tracheoles appear always to contain air as far as they can be resolved with the microscope.

The Diffusion Theory of Insect Respiration. The next problem in the physiology of the tracheal system is how oxygen is conveyed to the tissues. Although the tracheae are permeable to oxygen throughout their length, the abundant supply of tracheal capillaries in and around the most active tissues leaves no doubt that most of the oxygen enters the organs through these endings ; and the problem resolves itself into how oxygen is conveyed from the spiracles to the tracheoles. It was suggested long ago by Treviranus, and later by Thomas Graham (to whom we owe the laws of diffusion of gases), that it must be conveyed by diffusion. But to the superficial observer of these fine tracheal tubes, this idea seemed so inherently improbable that various other hypotheses were put forward, and it is only within recent years that the diffusion theory of insect respiration has been generally accepted. The present acceptance of this theory is due to the work of Krogh [162], who, taking into consideration the mean diameter and length of the tracheae, the oxygen consumption of the insect, and the diffusion coefficient of oxygen, calculated what difference in partial pressure between the atmosphere and the tracheal endings would be necessary to maintain the supply of oxygen that was actually consumed. He obtained the surprising result that, even in the case of large caterpillars, the partial pressure of oxygen at the tracheal endings need not be more than 2 or 3 per

cent. below that in the atmosphere; showing that diffusion alone was adequate to supply the needs of the insect.

The same argument applies to the elimination of carbon dioxide. The amount of carbon dioxide produced by the insect is usually rather less than the oxygen taken in; their rates of diffusion, being proportional to the square roots of their densities ($\sqrt{22}$: $\sqrt{16}$), are not enormously different. Therefore, since diffusion alone will account for the supply of oxygen, it will account equally for the elimination of carbon dioxide. But carbon dioxide diffuses through animal tissues, and therefore presumably through the insect cuticle, something like thirty-five times more rapidly than oxygen [282]. Consequently, since carbon dioxide liberated in the tissues must diffuse equally in all directions, the amount of this gas which will escape directly through the cuticle of the body wall (especially when this is thin) and through the walls of the larger tracheal trunks [69], must be far greater than the amount of oxygen that will enter by these routes. It is probably safe to say that in most terrestrial insects almost all the oxygen is taken in by the tracheae; in the case of *Dixippus*, it has been shown that about 25 per cent. of the carbon dioxide escapes through the skin, and in larvae of *Dytiscus* and *Eristalis* somewhat less [49].

The Function of the Spiracles. This simple conception of tracheal respiration is complicated by the need for retaining water; for most of the evaporation from an insect takes place through the spiracles [109, 188]. Burmeister discovered that each spiracle is provided with an occlusive mechanism, the main function of which is probably to protect the insect from loss of water: the adult flea, which has well-developed sphincters in the spiracles, is far more resistant to desiccation than the larva which has none [186]. Normally, the spiracles are kept closed; being opened only just often enough to keep the

insect supplied with oxygen. But when the insect is active, or when the rate of metabolism is increased through a rise of temperature, they are widely dilated [115]. Consequently, as the temperature rises, the rate of water loss from an insect tends to increase out of all proportion to the evaporating power of the air [109]. And if the insect at rest is caused to keep its spiracles permanently open, by exposure to nitrogen or carbon dioxide, its rate of loss of water is enormously increased [188].

This function of the spiracles has been termed the 'diffusion control' of insect respiration [115]. It is said to be effected chiefly by the local action of carbon dioxide upon sensory nerve endings in the spiracles themselves. But this cannot be the whole story, for the spiracles are caused to open in an atmosphere of nitrogen [115]. Their opening is therefore influenced by lack of oxygen as well as by excess of carbon dioxide. Presumably, oxygen-want exerts its action by the accumulation of acid metabolites, which stimulate the respiratory centres innervating the spiracles; and it is probable that carbon dioxide, in virtue of its acidity, may also stimulate these same centres.

Ventilation of the Tracheal System. This type of respiratory system, dependent solely upon gaseous diffusion, is adequate for most small insects, and even large insects if they are relatively sluggish; but it is insufficient for actively running or flying species with a high rate of metabolism and a massive production of energy. In these, in the larger Orthoptera and beetles, in bees, wasps and flies, a greater or less degree of mechanical ventilation of the tracheal system is superadded. We have seen that the spiral folding of the typical tracheae renders them resistant to collapse under pressure; but, in some cases at least, they can be expanded and contracted in their long axis like an accordion [282], and their capacity reduced by as much as 20 to 30 per cent.[69]. In other

cases they are not round in cross-section but elliptical (*Dytiscus* larva) or even ribbon-like (in the thorax of Muscid flies) and will then readily collapse when the pressure around them is increased. Or they may have thin-walled cavities at intervals along their course (as in *Melolontha*), or large dilatations ('air sacs') which occupy a great part of the body cavity (as in many Orthoptera, Hymenoptera, &c.) (Fig. 5, B) [39].

There is little doubt that, as Treviranus suggested, the main function of these collapsible tracheae or air sacs is the ventilation of the respiratory system. Like the ventilation of the lungs of vertebrates, the filling and emptying of these air sacs is secondary to the respiratory movements of the rigid body wall which encloses them. When the body wall is in the inspiratory position they are widely open; in the expiratory position many of them are collapsed and empty [69]. In addition they are doubtless ventilated to some extent by general movements of the body —for example, during flight; and where they lie in rigid portions of the body, such as the head, they are ventilated, as Graber pointed out, by the transmitted pressure of the blood.

The result of this process is that the greater part of the tracheal system is kept filled with a gas which approximates in composition to the outside air; but the actual supply of oxygen to the tissues again takes place by diffusion along the tracheal branches given off by the air sacs. This, of course, is analogous to what happens in vertebrates, where only the upper parts of the respiratory tract are ventilated mechanically, exchanges in the alveoli of the lung being dependent on diffusion. The extent to which the tracheal system is ventilated mechanically varies enormously in different insects, and in the same insect according to its physiological state; but in many cases the efficiency of the process compares very favourably with the ventilation of the human lungs.

For instance, in *Melolontha* the respiratory system may be emptied during expiration of about one-third of its total capacity [69] (the total capacity being 39 per cent. of the body volume !), and in the larva of *Dytiscus* of about two-thirds [162]. (In quiet respiration in man, the lungs are emptied of about one-seventh of their total capacity ; the most extreme degree of ventilation empties about two-thirds.)

(In addition to their ventilating function, the tracheal air sacs of insects sometimes serve a purpose like the air-containing sinuses in the facial skeleton of mammals, or the pulmonary air sacs in the bones of birds ; thus, by extending into the massive head and mandibles of certain beetles, they permit an increase in the skeletal bulk without adding to the insect's weight [282].)

The respiratory movements of insects are brought about by a special musculature which varies greatly from one group to another [9]. As a general rule the movements are confined to the abdomen, but in *Dytiscus* and *Hydrophilus* ventilation is maintained by aspirating movements of the metathorax, the abdominal movement apparently being passive [40]. In most cases expiration is active and inspiration passive, though in the larva of *Aeschna* and in the grasshopper expiratory muscles also are present [282]. The movements may consist of dorso-ventral flattening movements (Orthoptera, Coleoptera) or longitudinal telescoping movements (Diptera, Hymenoptera).

The simplest interpretation of these movements is that they are ventilating all parts of the tracheal system alike. But if, during the respiratory contraction, the spiracular valves in different parts of the body open and close independently of one another, it is possible that a directed stream of air will be driven through the tracheal system—certain spiracles serving always for inspiration, others for expiration—an arrangement which would serve to enrich the air in

the inspiratory section of the system. The idea that such a circulation of air does occur has often been put forward [282], but only in recent years has it been convincingly demonstrated. Thus, it has been shown that if the four anterior pairs of spiracles in the locust (*Schistocerca*) are enclosed in one gas chamber, and the six posterior pairs in another, air is actively transported during respiration from the anterior to the posterior chamber [90, 181]. The underlying principle of this mechanism is that the rhythmical nervous impulses which control the ventilating movements are co-ordinated with impulses which bring about the synchronous movement of the spiracles—some of these opening during inspiration, others during expiration [90]. But before looking further into this point, we must consider the control of the ventilating movements themselves.

The Regulation of Respiration. The respiratory movements are effected by impulses from nerve centres. These centres are of two kinds [239]: so-called primary respiratory centres which lie in the segmental ganglia and control the movements of their own segments (for the isolated segments of the abdomen may perform respiratory movements) [9], and secondary centres which have an overriding action and control the movements in the whole insect. One might expect the secondary centre to lie in the head but this seems never to be the case: decapitation produces only a temporary and uncertain effect on respiration [282]. In the few insects that have been studied, it is situated in the prothorax [239].

The isolated ganglia of insects which possess a mechanical ventilation of the tracheal system (*Dytiscus*, *Aeschna*) show rhythmical changes in electrical potential of the same frequency as the respiratory movements of the intact insect [2]. There must, therefore, be a spontaneous respiratory rhythm inherent in the nerve centres. But the activity of the centres, both in rate of rhythm and depth of move-

ment evoked, may be influenced by external stimuli, either nervous or chemical [90]; and during times of rest the ventilating respiratory movements may cease altogether [115]. There is evidence that during the onset of activity—flight, for example—the respiratory movements may sometimes be initiated by nervous stimuli alone [90] (for any stimulus will cause an increase in respiration in insects) [239]; but they can also be initiated by chemical stimuli alone [115]; and, although there must be endless variation in different species, perhaps these play the greater part in the normal life of the insect.

Either a lack of oxygen [9] or an excess of carbon dioxide [239] may stimulate the respiratory centres and cause hypernoea; in some insects an excess of oxygen may cause a prolonged apnoea [9]. Now excess of oxygen will not diminish the production of carbon dioxide; nor will a lack of oxygen increase it. If, therefore, carbon dioxide were the *sole* respiratory stimulant, respiration should not be influenced by the tension of oxygen. But there is no doubt that carbon dioxide *can* control respiration: in *Dixippus*, the activity of the secondary or prothoracic centre is stimulated by carbon dioxide tensions of 0·2 to 3 per cent.; the primary centres respond to 12–15 per cent. [239]; and in the *Periplaneta* and other insects, ventilation begins, even in the insect at rest, at a carbon dioxide tension of 10 per cent. [115] Since it is reasonable to assume that the chemical factor at work is the same in all these cases, it seems probable that this factor is the acidity in the nerve centres—due either to an excess of carbon dioxide, or to acid metabolites accumulating in the absence of oxygen [239]. But some authors believe that there may be receptors (which have not been demonstrated histologically) in the tracheae, which respond to the gas these contain [239].

We have seen (p. 20) that in thin-skinned insects much of the carbon dioxide diffuses through the

general surface of the body, and therefore cannot serve as a respiratory stimulus at all. Thus we find that mosquito larvae, and the larvae of *Aeschna* and *Dytiscus*, are driven to seek air at the water surface by oxygen want and not by carbon dioxide excess [162, 282]. On the other hand, the leg movements in the aquatic bug *Corixa*, which direct a stream of water over its air store (p. 28), are called forth by the accumulation of carbon dioxide; while the same insect is caused to rise to the surface when the air store is reduced to a given size [32].

We are now in a position to revert to the question of the stream of air directed through the tracheal system by the co-operation of ventilatory and spiracular movements. In the light of recent work there is no reason to doubt that such a directed flow does often occur. But its existence implies that the spiracular opening is being centrally controlled by an extremely complex nervous mechanism which synchronizes this movement with the ventilation [90]. Now we have seen that the spiracles are normally chemically controlled [115]. This chemical control may be quite local in its action; in the sense that those spiracles which serve the most active parts of the body may show rhythmical opening and closing while the remainder of the spiracles stay closed [180]. Consequently, it must always be a matter of difficulty to decide whether, in a given insect, the occurrence of a directed stream of air through the tracheal system is a purposive movement co-ordinated by a higher respiratory centre, or whether it is a purely accidental result of the simultaneous occurrence of a ventilating rhythm determined by the state of the higher

FIG. 5.—Some types of respiratory system in insects schematic

A, simple anastomosing tracheae, with sphincters in the spiracles (p. 16). B, mechanically ventilated air sacs developed (p. 22). C, metapneustic respiration: only terminal spiracles functional (p. 28). D, tracheal system entirely closed: cutaneous respiration (p. 29). E, the same with abdominal tracheal gills (p. 30). F, the same with rectal tracheal gills (p. 30).

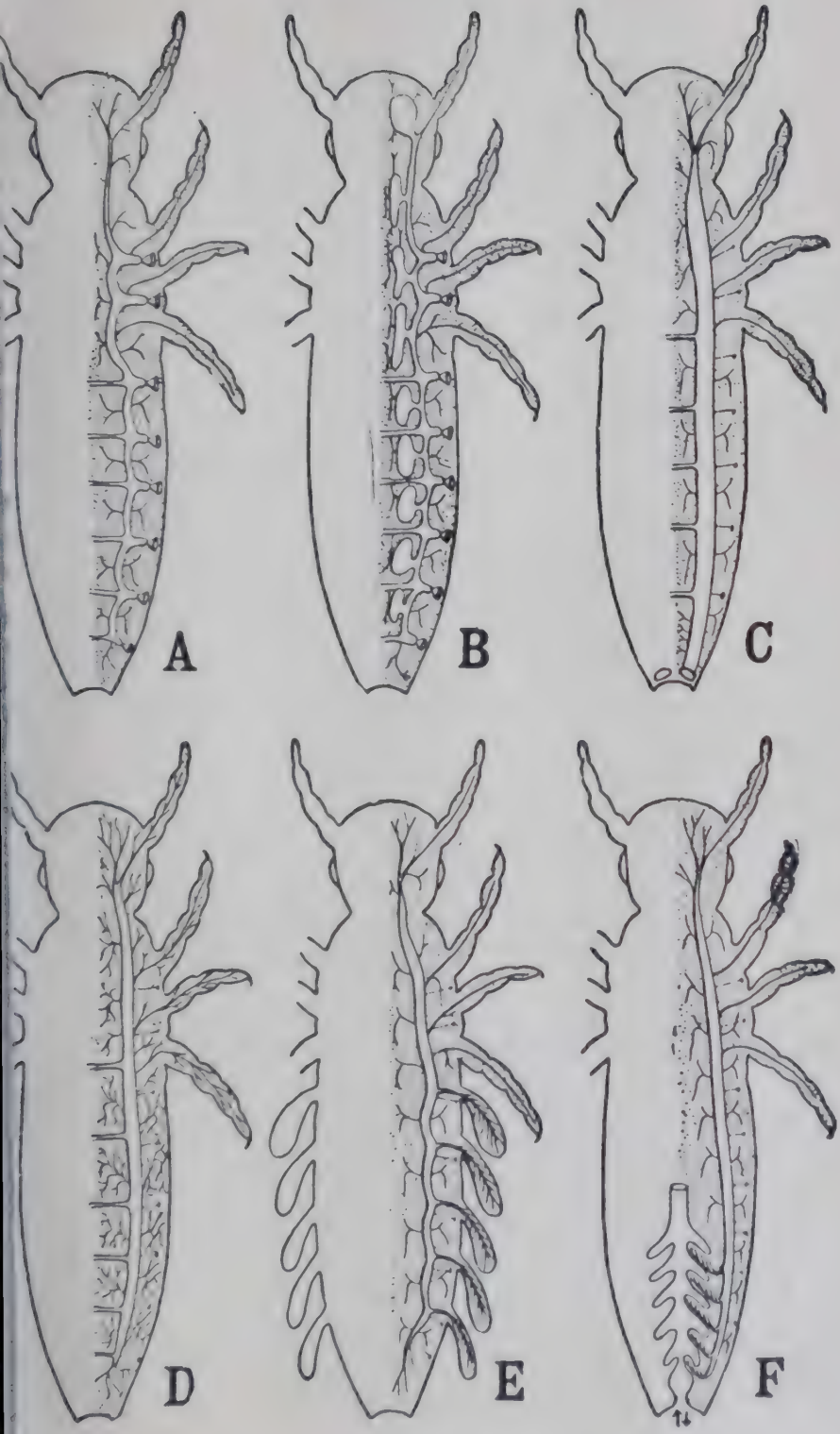

FIG. 5.

respiratory centre, and a spiracular rhythm determined by the local needs of different parts of the body [180, 181]. To decide between these alternatives will need very careful study in each insect.

Respiration of Aquatic Insects. The majority of insects that are aquatic in the adult stage breathe gaseous air like the terrestrial forms; but they develop special structural modifications to enable them to do so. Since all the spiracles cannot be exposed to the exterior, there is a tendency for the respiratory function to become concentrated at one end of the body. In *Hydrophilus*, the mesothoracic spiracles are the most important; in *Dytiscus* and its allies and in the aquatic Hemiptera, the last abdominal spiracles predominate [64]. In many larvae (*Dytiscus*, Culicidae and many other Diptera) the other spiracles have become obliterated, or at least functionless, and the insects breathe entirely through the terminal spiracles ('metapneustic' respiration) (Fig. 5, C). In all these cases, in the antennae of *Hydrophilus*, in the abdominal fringes of hair in *Notonecta*, in the elytral surface itself in *Dytiscus*, and around the tracheal orifices of the metapneustic larvae, there are hydrofuge structures that enable the air-containing regions of the body to break through the surface film and obtain communication with the atmosphere [282] (see p. 6).

In many cases (mosquito larvae, *Dytiscus* larvae, &c.) the tracheal trunks are so capacious that they serve as stores of air, and enable the insect to remain submerged for a considerable time. In other insects, a store of air is carried beneath the elytra (in *Dytiscus* &c.) or over the ventral surface of the body (in *Notonecta*, *Corixa*, &c.) by means of the hydrofuge surfaces and hairs already discussed (p. 6). These external air stores have several functions: (1) They have an important hydrostatic function in enabling the insect to reach the water surface in the correct position to take in oxygen [282]. (2) They provide a

store of oxygen which is gradually used up by the submerged insect; for example, the oxygen in the elytral air of *Dytiscus* may fall from 19·5 per cent. at the moment of diving, to 1 per cent. or less in three or four minutes [282]. (3) They provide a mechanism for obtaining dissolved oxygen from the water, and so function as a kind of physical gill [76]. For the invasion coefficient of oxygen between water and air is more than three times as great as that of nitrogen. Consequently, as the partial pressure of oxygen in the air store becomes reduced, equilibrium will be restored by the diffusion of oxygen inwards, rather than by the diffusion of nitrogen outwards. Of course, some nitrogen will diffuse out, but as long as any remains undissolved the process can go on, and the insect can extract dissolved oxygen from the water. This mechanism is of more or less value to all aquatic insects that carry air stores; and small forms like *Corixa* can obtain enough oxygen in this way even at summer temperature so long as they do not swim actively. The striking effect of the process may be shown by quoting a single experiment: *Notonecta* lived five minutes submerged in water saturated with nitrogen, thirty-five minutes in water saturated with oxygen, but six hours in water saturated with atmospheric air—the air store, in each instance, being first charged with the dissolved gas [76].

By the provision of air stores which cannot be replaced by water, a few insects have become independent of the atmospheric air; but this has happened very rarely [282]. On the other hand, by the obliteration of all the spiracles of the respiratory system, and the development of gills, many insect larvae have become completely adapted for the respiration of dissolved oxygen [64]. In many cases, the general surface of the larva, richly supplied with fine tracheae, provides the respiratory surface (in *Chironomus*, *Simulium*, *Corixa*, &c.) (Fig. 5, D). Sometimes there are specialized plate-like projections rich in tracheae

(Ephemeridae, Plecoptera) (Fig. 5, E); or papillae from the anus, consisting of little more than massed tracheal branches covered by a thin cuticle (*Elmis*, Col.); or a network of tracheae inside the rectum (as in the larvae of Anisopterid dragon-flies) (Fig. 5, F); or rigid cuticular filaments containing air, which do not collapse on drying, and can therefore serve for respiration both in water and on land (as in the pupa of *Simulium*, and other Diptera from mountain torrents [215]).

In some cases the oxygenation of these organs is ensured by a highly developed respiratory centre: the gill plates of Ephemeridae are violently agitated in water poor in oxygen [9], and the rectum of *Aeschna* is ventilated by abdominal movements controlled by primary and secondary respiratory centres (p. 25) [239]. It has been shown that the partial pressure of oxygen in the closed system of these insects is aways less than its tension in the surrounding medium, and that of carbon dioxide greater; it is therefore generally believed that the exchange of gases through these gills is effected solely by diffusion [282].

In addition to these undoubted gills, there are, in many aquatic insect larvae, tubular out-growths from the body surface which may contain blood only, or blood with a rather sparse supply of tracheae. These structures are called blood gills; but what experimental evidence exists seems to point against their having any but a subsidiary function in respiration [114, 253]; though in the present state of knowledge it would be unwise to generalize [266]. In one case, that of the anal papillae of the mosquito larva, they have been shown to be chiefly water-absorbing organs (p. 68) [285].

We have seen (p. 28) that the external air stores carried by aquatic insects help to control their equilibrium in the water. The air in the tracheal system, also, must often be of some importance for this purpose; and in the pelagic larva of *Corethra* there are

developed four large air sacs which function solely as hydrostatic organs. This larva can adjust its specific gravity to that of the water it is in by varying the capacity of these air sacs—apparently by some active change which causes expansion or contraction of their cuticular walls [282].

Respiration of Parasites. The internal parasites of insects, which live a semi-aquatic life within the blood and tissues of their host, naturally show many of the respiratory adaptations possessed by aquatic larvae. In the young stages of many of them the tracheae do not contain air, and oxygen simply diffuses from the blood of the host into the blood of the parasite—as it does in the young aquatic larva of *Chironomus* (Dipt.) and *Acentropus* (Lep.), &c. Later, when air has appeared in the tracheae, these commonly supply a rich network of branches to the skin—as they do in the older aquatic larvae of *Simulium*, *Chironomus*, &c. There are often outgrowths from the body surface, usually from the tail, which recall the gill-like organs of aquatic forms. Sometimes these structures are well supplied with tracheae (as in the larva of *Cryptochaetum* (Agromyzidae : Dipt.)) [251] or with circulating blood (as in *Apanteles* (Braconidae : Hym.)) and are of proved importance in respiration ; but in most cases their respiratory significance is very doubtful and their function is problematical [252]. Finally, the metapneustic type of respiration common in aquatic insects is seen in most Dipterous parasites (Tachinidae, &c.), which pierce the body-wall or the large tracheal trunks and breathe the atmospheric air. The habit of attaching themselves to the tracheal tubes recalls the fact that certain aquatic larvae (of the beetle *Donacia* and the mosquito *Mansonia*) possess specially modified respiratory siphons which they insert into the air-containing tissues of aquatic plants, and are thus able to remain permanently beneath the water surface [282].

CHAPTER III

THE CIRCULATORY SYSTEM AND THE BLOOD

IN the insect body there is only one tissue fluid, the blood or haemolymph, occupying a single cavity, the haemocoel, and freely bathing all the tissues. With few exceptions, there is only one blood-vessel, which runs along the mid-line of the back. The posterior segment of this pulsating vessel, the 'heart', is provided with a series of valved openings or ostia through which the blood can enter; the anterior segment, the 'aorta', is a uniform contractile tube. After passing through the brain above the oesophagus, the aorta ends more or less abruptly [91]; and from this point the blood simply percolates slowly backwards through the tissues. But in many insects it is still subject to some direction: the aorta may discharge into definite vessels carrying the blood in different directions [40]; the antennae and limbs are often divided by longitudinal membranes, the blood entering the limb on one side and leaving on the other; and the abdominal cavity in some insects is divided by two horizontal membranes, the dorsal and ventral diaphragms, into three sinuses: the pericardial sinus containing the heart, the perineural sinus containing the nerve cord, and the visceral sinus between. The perineural sinus tends to conduct the blood to the posterior end of the abdomen before allowing it to return to the heart; but it is perforated and incomplete laterally, so that some of the blood circulates transversely across the abdomen below it. The dorsal diaphragm,

when present, is also fenestrated, and thus allows the blood to enter the pericardial sinus throughout its length (Fig. 6).

The Mechanism of the Circulation. In insects with a rigid cuticle, the blood in the body cavity, when the insect is at rest, is at atmospheric pressure (Odonata [232]) or even less (*Dytiscus* [40], *Apis* [91]). In the more soft-bodied insects, the general pressure may be raised (to 40 or 50 mm. of water in the larva of *Aeschna*, or even more during exertion [232]) by the muscular tension of the body-wall. The pressure may be increased, also, during the ventilation of the tracheal system ; and during those special acts which are brought about by the displacement of the blood, such as the expansion of the wings in emerging adults (p. 13), the general pressure may be maintained for a prolonged period at a high level (75 mm. of water in the dragonfly [232]).

But, like the blood in the vena cava of mammals, the blood of insects is always aspirated, into the heart, during diastole, under a negative pressure : a pressure less than that existing in the general body cavity. This force is due partly to the elastic muscular walls of the heart itself [73], partly to the elastic traction of the dorsal diaphragm which is tied to the lower wall of the heart [40], and partly to the contraction of the muscle fibres (the aliform muscles) which commonly occur in the substance of this diaphragm [73]. During systole, a weak positive pressure develops and the blood is driven forwards.

In some insects, such as the larvae of Nematocera [73] and the Ephemeridae [190], the valves of the ostia have become so modified as to form interventricular valves ; these divide the heart into a succession of chambers through which the blood can flow only forwards. But this arrangement is the exception ; in most insects the heart is patent throughout its length and acts as a whole [101], the blood being carried along it by peristaltic waves. As a rule, such waves start at the

hind end of the heart and pass forwards; but in many insects [101, 211] the direction of beat may be periodically reversed, and the blood then escapes into the abdominal cavity through the relaxed ostia. Sometimes beats may arise at a number of points

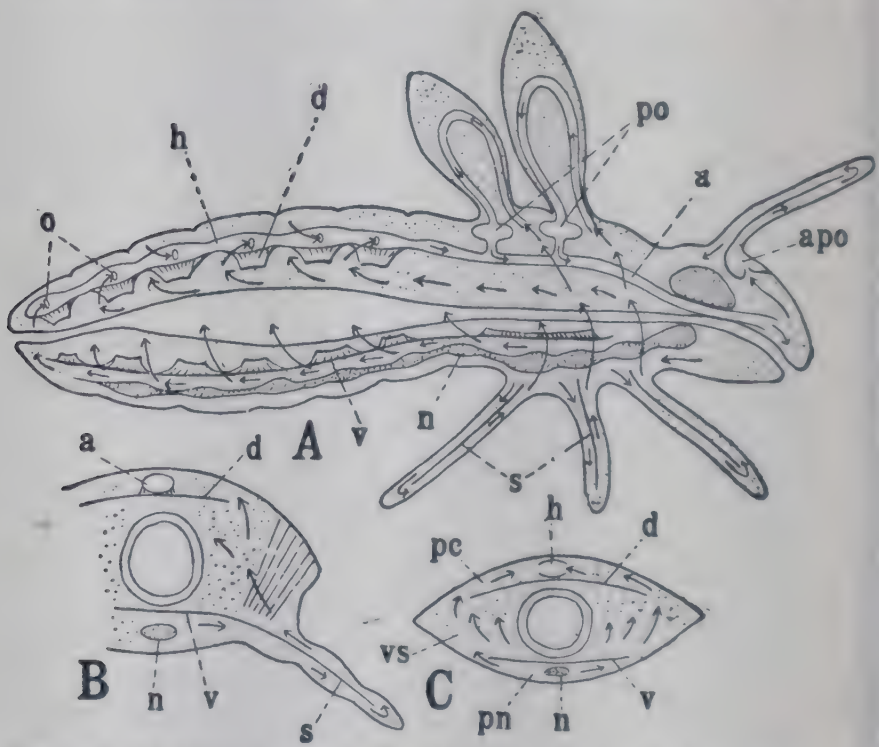

FIG. 6.—A, insect with fully developed circulatory system: schematic; B, transverse section of thorax of the same; C, transverse section of abdomen. Arrows indicate course of circulation. (Based largely on Brocher.)

a, aorta; *apo*, accessory pulsatile organ of antenna; *d*, dorsal diaphragm with aliform muscles; *h*, heart; *n*, nerve cord; *o*, ostia; *pc*, pericardial sinus; *pn*, perineural sinus; *po*, meso- and metathoracic pulsatile organs; *s*, septa dividing appendages; *v*, ventral diaphragm; *vs*, visceral sinus.

simultaneously and extinguish one another when they meet [73].

Thus the circulation of the blood is secured primarily by the work of the heart, which aspirates it from the abdominal cavity and pumps it forwards to the head. In the thorax, accessory pumps are

often present [40]. These aspirate blood from the thoracic cavity, through certain of the wing veins, and return it through connecting vessels either to the aorta itself (*Dytiscus*, *Aeschna* larva, *Sphinx*) [39] (Fig. 6, A) or to the body cavity again (*Tabanus*, Dipt.; *Vespa* [39], *Apis*, Hym. [91]). Accessory pumping organs may irrigate the antennae (*Periplaneta*, Hymenoptera, &c.[91]) and the legs (Hemiptera) [111]. But in many insects these structures are wanting, and the circulation through the appendages is then effected (i) partly by their own muscular movements, (ii) partly by the pressure changes in the abdomen brought about by the respiratory movements (*Aeschna* larva [40], Ephemeridae larvae [190])—in which case the pulse beats in the leg synchronize not with the heart-beat but with the respiratory contractions, and (iii) partly owing to the fact that the efferent stream (in the posterior chamber of the limb) communicates with the perineural sinus, where the pressure is higher, while the afferent stream (in the anterior chamber) communicates with the perivisceral sinus, where the pressure is lower: the blood in the limb is thus subject to the aspirating action both of the heart and of the pulsatile organs of the thorax [40] (Fig. 6, B). Finally, in those insects in which the ventral diaphragm is well developed (many Orthoptera, Hymenoptera, Lepidoptera), it may contain muscle fibres, and by means of wave-like contractions may actively assist in driving the blood backwards and laterally [40].

Control of the Heart-beat. If the heart of the cockroach may be taken as a normal example, the heart of insects has a very complicated nerve supply [3]. Two lateral nerves, containing ganglion cells, and apparently constituting an intrinsic cardiac ganglion, run along its entire length, and are connected in front with the ganglia of the visceral nervous system. In addition, the heart receives sensory and motor nerve fibres from the segmental ganglia of the ventral chain.

There is no doubt, therefore, that the heart enjoys a large degree of nervous control ; experimentally, faradic stimulation in the region of the neck gives rise to accelerating impulses which reach the heart both by the lateral nerves and by the segmental branches from the ventral cord [241]. What is less certain is whether the automatism or spontaneous pulsation of the heart is a property of the muscles (myogenic) or of the nerves (neurogenic). An important factor in the initiation of each beat appears to be the tension in the muscular wall of the heart, due either to the contraction of the aliform muscles (which, in a given segment, may precede the contraction of the heart itself) or to the constant elastic tension which these structures exert [73]. If the aliform muscles are cut through, the heart no longer beats [73]. But it does not necessarily follow from this that the heart-beat is myogenic. It has been found that the change in rate of the heart-beat at different temperatures shows a 'temperature characteristic' or 'critical thermal increment' which agrees remarkably well with that of other vital activities which are controlled by the rate of discharge from nerve centres [241] ; and for those who regard such evidence as carrying weight, this suggests a neurogenic origin. Whatever the nature of the automatism, it is remarkably sensitive to carbon dioxide : the heart-beat in aquatic larvae is at once arrested in water saturated with this gas [88].

Composition and Properties of the Blood. The blood of insects may be a clear colourless fluid ; but more often it is tinged with green or yellow (p. 81). The specific gravity varies from 1·03 in the larva of *Deilephila* (Lep.) [119] to 1·045 in the larva of *Apis* [22]. The reaction is usually very slightly acid : pH = 6·4 in *Deilephila* larva [119], 6·6–6·8 in *Bombyx mori* [68], 6·83 in *Apis* larva [22] ; but it may differ slightly in the two sexes [68] and may vary with the age of the insect. Thus, in *Bombyx* it becomes more alkaline at each moult [68] ; and in *Apis* [22], *Deilephila* [119]

and other insects [179] it is more acid during the pupal stage. The blood is moderately well buffered; but the bicarbonate is very low [74] and the buffering appears to be due to the phosphate and, presumably, the protein. The molecular concentration, expressed as $\triangle$ ranges from 0·56 in *Saturnia* larva [74] to 0·78–0·81 in *Deilephila* larva [119], and 0·86–0·87 in *Apis* larva [22]; but the osmotic pressure can, apparently, become enormously increased temporarily by the accumulation of unoxidized metabolites during oxygen want [278]. On the other hand, those few insects which have colonized sea water appear to be homoiosmotic: the molecular concentration of their blood is unaffected by the outer medium [285]. Of the total molecular concentration, a surprisingly small part, sometimes not more than 4·2 per cent. and rarely more than 15 per cent., is chloride [74]; whereas the phosphate content, as compared with vertebrate blood, is very high, as are, also, the magnesium and calcium [36]. But the most striking feature is the high content of amino acids [22, 74], which may be twenty or thirty times as great as in human blood, and form nearly 15 per cent. of the total nitrogen [59]. In addition, there is a considerable amount of residual nitrogen in peptide form [119], while proteins (albumen and globulin) are present in much the same amounts as in human plasma. The glucose level is of the same order as in mammals [22, 119]. Urea is always present in small quantities [67]. Fat, which occurs largely as a very fine emulsion, varies with the state of digestion and nutrition [110].

The blood of many insects (*Apis* larva [22], &c.) does not clot; wounds are simply closed by a plug of cells. In others (cockroach, &c.) it clots very readily. The blood-cells send out fibrillar pseudopodia which interlace with one another to form a living network within which the fibrin filaments separate out; but the cells are said not to be necessary for clotting to take place, nor is calcium needed for the process [200].

Cytology of the Blood. The blood-cells or haematocytes of insects, as seen in preparations, present an extraordinary diversity of appearance; but this seems to be due to the protean forms which they can assume rather than to the abundance of distinct types. They multiply and grow in the body cavity throughout the life of the insect, appearing first as small darkly staining forms termed 'proleucocytes' [132, 211], which are often seen dividing and are not yet capable of phagocytosis. As they grow they become pyriform or spindle-shaped and will ingest dead bacteria, Indian ink, tissue débris, &c.; they are then called 'phagocytes'. Their appearance naturally varies very much with their content, and sometimes separate names have been given to these phases [137]; moreover, they have a habit of spreading themselves out in stellate form upon flat surfaces, such as the basement membranes, their aspect becoming totally changed [286].

These haematocytes are by no means all circulating; indeed, the majority adhere to the surface of the tissues; they collect particularly along the sides of the dorsal vessel, often in definite clumps termed 'phagocytic organs' [62]. The larvae of Chironomidae present a complete series in this respect: in certain genera only free haematocytes are present; in others, both haematocytes and fixed phagocytic cells occur; and in yet others there are no circulating cells at all but only phagocytic tissue [171]. The haematocytes become far more numerous during moulting [286] and metamorphosis [208], when they may play a part in removing the dead cells and tissues: during the metamorphosis of Muscids, these phagocytic cells (the 'Körnchenkugeln' of Weismann), stuffed with the products of histolysis, are exceedingly conspicuous. The phagocytic haematocytes will ingest, and in some cases destroy, living bacteria introduced into the blood [137]. They collect at the site of wounds and form a closing plug which forms the basis for the subsequent

healing process. They will congregate in great numbers around foreign bodies [172, 218] and certain parasites, walling these off in a discrete capsule; sometimes the cellular nature of this capsule persists [135], but more often the cell bodies become converted into homogeneous membranes from which the nuclei disappear ; and it is possibly in this way that the connective tissue membranes which cover the organs of insects are formed [172]. In some insects, haematocytes laden with conspicuous granules (granular leucocytes) [132] are present in the blood ; although these are no longer phagocytic they seem to represent a stage in the life history of these same cells.

Besides this type of cell with all its varied powers, there is, in most insects, another type which is equally distinct. It has a rounded or oval form, the cytoplasm is generally eosinophil, and it takes no part in phagocytosis [132] nor in the formation of encapsulating membranes [172]. In appearance these cells are like diminutive oenocytes ; and on this account they are often called ' oenocytoids ' ; but they do not seem to bear any relation to the true oenocytes [286]. Their function is quite unknown : they increase in number during moulting [286], like the phagocytes ; and they collect around foreign bodies in a zone peripheral to the phagocytes themselves [172].

Finally, in certain Hemiptera, there are blood-cells laden with fat globules, ' adipoleucocytes ', and others charged with wax ; but the relation of these to the types described above is uncertain [132].

The Functions of the Blood. (i) *Mechanical.* The blood plays an important part in transmitting pressure from one region of the body to another : the hatching of many insects from the egg (p. 13), the rupture of the old skin at moulting (p. 12), the expansion of the wings in the newly hatched adult insect (p. 13) and many other movements are brought about by the localized pressure of the blood.

(ii) *In Nutrition.* The blood conveys the nutrient

materials to the tissues, and the waste products to the excretory organs. The precise part that it plays in these functions is not really understood, but it is probable that the composition of the blood may vary enormously with the state of nutrition and, notably, during moulting and metamorphosis when many of the larval tissues are breaking down and the cells of the fat body are yielding up their protein and fatty contents. The blood must also be regarded as an important reserve of food material: in the larva of *Deilephila*, during fasting, the protein in the blood is rapidly consumed; and during pupal life in the same insect more than half the total energy metabolism is effected at the expense of the blood [119].

(iii) *In Immunity.* The phagocytic blood-cells provide perhaps the chief mechanism for protecting the insect from bacterial invasion [54, 137]; but humoral immunity, both natural and acquired, does occur [54]. The discussion of these matters would take us too far afield.

(iv) *In Respiration.* We have already seen that oxygen is ordinarily conveyed directly to the tissues by the tracheal system. But many cells are separated from the nearest tracheal tubes by an appreciable space; sometimes, notably in the pupa, organs may be entirely devoid of tracheal supply; and in some aquatic insects the tracheal system is completely filled with fluid. Moreover, the tracheal system, throughout its length, is permeable to oxygen, which must therefore escape into the blood. Under all these circumstances [282], the blood acts as a carrier of oxygen. There are, also, here and there among insects, special arrangements of the tracheal system which seem to be designed to aerate the blood: a convoluted tract in the aorta of the honey-bee is richly supplied with tracheae [91]; the posterior region of the heart in the metapneustic larvae of Nematocera is often surrounded by a basket-work of tracheoles [282]; and in the thorax of *Nepa* is a peculiar organ so

chly supplied with tracheae and bathed with blood s to suggest that it may be a kind of tracheal lung [111]. In view of these relations the question naturally rises whether the blood of insects contains chemical arriers of oxygen comparable with the haemoglobins nd haemocyanins of other animals. With a single xception, this has not yet been proved to be the ase. In those insects, such as the larva of the honey-ee, in which the properties of the blood have been ost carefully studied, it has not been found to take p more oxygen than can be accounted for by physical olution [22]; but it must be admitted that such in-estigations have not yet been very extensive. The ngle exception is in the larvae of certain Chirono-idae, which contain haemoglobin in the blood in ee solution—that is, not in corpuscles. The affinity f this haemoglobin for oxygen is, however, very ifferent from that of mammals. At all ordinary nsions of oxygen it remains fully saturated; and only begins to liberate its oxygen when the pressure f this gas is reduced to 1 per cent. of an atmosphere r less; the precise level varying in different pecies [114]. In other words, it is capable of acting s a carrier only under conditions of extreme paucity f oxygen and seems, in fact, to be a special adaptation o life in poorly oxygenated waters—the larvae that ontain haemoglobin being much less susceptible to xygen want [282].

We have seen, also, that the blood probably plays considerable part in the carriage of carbon dioxide om the tissues (p. 20). But here again there seems o be no chemical provision for its transport; the icarbonate and the carbon dioxide capacity of insect lood are both very low [22, 74].

CHAPTER IV

DIGESTION

INSECTS feed upon almost every type of organ substance found in nature [259]: some on plant others on animals; some on the sap of plants or th tissue fluids of animals, others on foliage, or flesh dry timber, or hair and feathers; some on fungi the live and dead bacteria in the excrement of animal others on the sterile juices of living forms. The feeding mechanisms, and the structure and chemistr of their digestive system present, therefore, the mo extraordinary variety, and it becomes singularl difficult to sift out the general principles in the physi logy of their nutrition.

The Alimentary Canal. With the exception the earliest stages of some parasitic insects, whic absorb nutriment through the general body surface [2 all insects take their food into an alimentary can This consists always of three parts: the fore-gu mid-gut and hind-gut. The fore-gut and hind-gut a both lined with cuticle; in the mid-gut the cells a freely exposed; from which it follows that secretion digestive juices can occur only in the mid-gut, a here, also, at least the greater part of absorption u doubtedly takes place. In many insects the secreti of the mid-gut is supplemented by that from th salivary glands, mixed with the food before it swallowed.

Fig. 7 shows some of the commoner types of inte tinal system, and the different uses to which th parts are put. In the most primitive insects, and

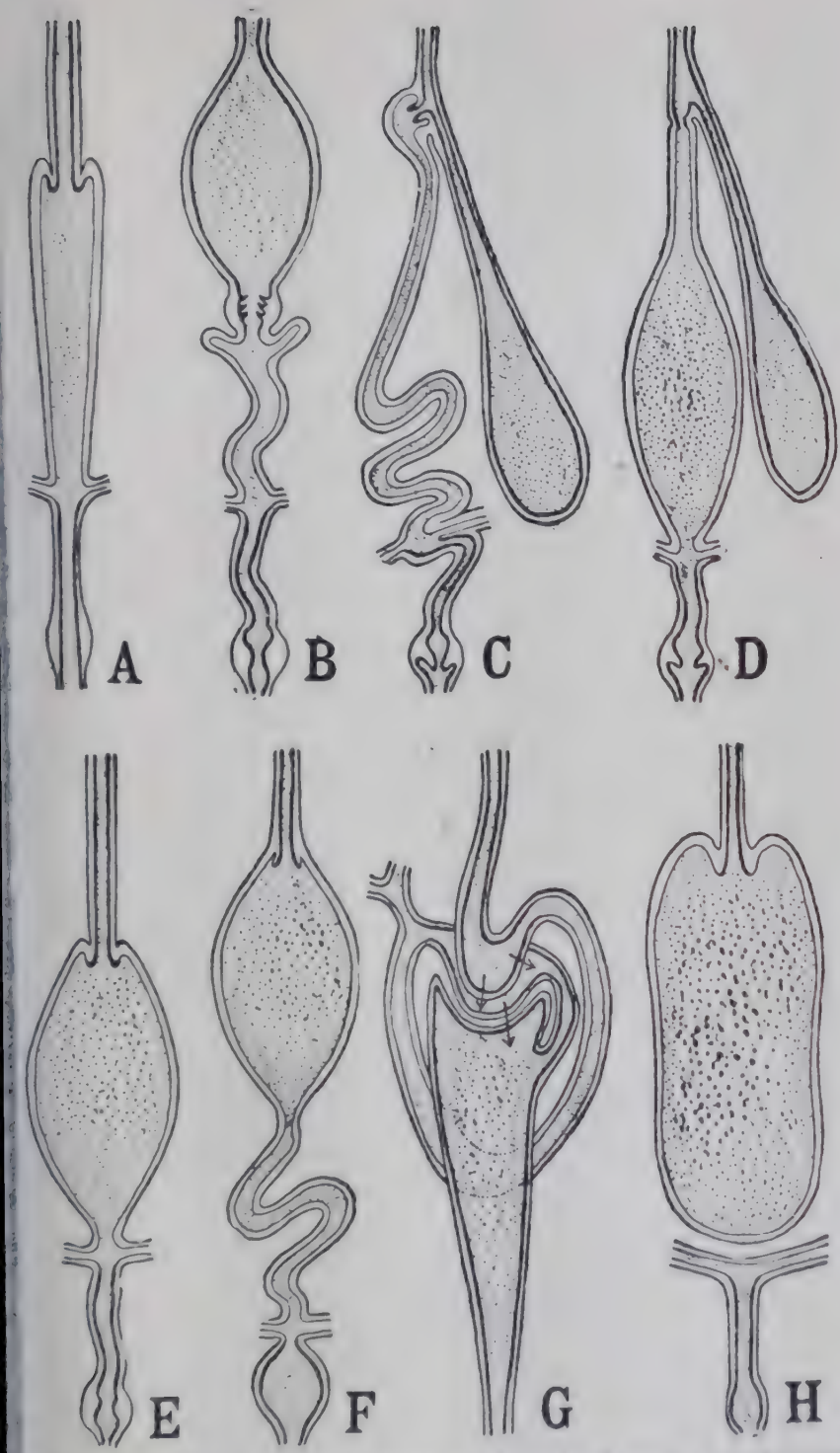

FIG. 7.—Types of alimentary system in insects: schematic. Fore-gut and hind-gut indicated by a heavy line internally. Explanation in text. (G modified after Weber.)

many larval forms (Diptera–Nematocera, Lepidoptera, Tenthredinidae and many Coleoptera) (Fig. 7 A), the fore-gut or oesophagus has no other function than to conduct the food into the mid-gut; from which it is passed on, often more or less continuously, to the hind-gut. But in very many insects (Dermaptera, Orthoptera, Isoptera, Odonata, Hymenoptera, many Coleoptera), the hinder part of the fore-gut is dilated to form a capacious crop (Fig. 7, B). Here the food is stored before being transmitted, in small quantities at a time, to the mid-gut. It is, however, not only stored but digested, being acted upon always by the salivary secretion, and, at least in the Orthoptera, by the digestive juices passed forward from the mid-gut [247]. In the higher Diptera a crop for storing food is again present (Fig. 7, C), but it takes the form of a diverticulum connected to the fore-gut by a narrow duct. The food in this crop is mixed only with saliva, and it suffers very little digestion until it is transferred to the long coiled mid-gut. In the Lepidoptera, and in many Diptera (Culicidae, Tabanidae [281]) (Fig. 7, D), the ingested food goes straight to the mid-gut and is there both stored and digested; the 'crop' has all but lost its function as a food reservoir, and is used chiefly (in many Lepidoptera, solely) to receive the air swallowed by the insect when it emerges from the pupa (p. 13). In the fleas (Siphonaptera) and sucking lice (Siphunculata) the crop has been lost entirely (Fig. 7, E), and the food is taken straight into a voluminous stomach where it remains until digestion is complete.

In many Diptera the mid-gut consists of several segments characterized by differences in the epithelium; the more anterior being concerned probably only with absorption, the more posterior with digestion [277]. The value of this arrangement when the insect takes in much fluid with its food is obvious; for much of the water and many of the assimilable constituents are removed before the food reaches the

digestive juices, and consequently these juices do not suffer unnecessary dilution. In many Heteroptera, this arrangement has gone a stage further; there is once again a capacious crop in which the meal is received, but it is a crop composed of mid-gut. In the blood-sucking forms (*Cimex* and *Rhodnius*) (Fig. 7, F), the food is not at all digested in this part of the mid-gut, but is merely concentrated by the removal of fluid, and the concentrated product passed on for digestion to the long narrow intestine [288]. In these insects the fluid that is absorbed passes into the blood and is then excreted by the Malpighian tubes [176, 283]; but an advance on this mechanism has been developed by many Homoptera (Coccidae, &c.). These feed on the juices of plants, and therefore receive a great excess both of water and of sugars. But instead of the superfluous fluid being taken into the blood and then eliminated by the Malpighian tubes in the manner just described, a dilated loop of the fore-gut, the 'filter chamber', with very delicate walls, is invaginated into the rectum (Fig. 7, G); the unwanted fluids are here absorbed, or perhaps simply filtered, directly into the terminal part of the hind-gut; and so come to be discharged again to the exterior as honey dew, manna, and such-like products [268]. Many modifications of this arrangement have been described [268].

Another special modification of the gut is met with in the larvae of Hymenoptera-Apocrita, and in the larvae of *Myrmeleon* and other Neuroptera (Fig. 7, H). In these the mid-gut remains unconnected with the hind-gut until the time of pupation. Consequently, the stomach becomes enormously distended with the undigested residue of the food, which is not evacuated until just before pupation [19].

The Proventriculus. In nearly all insects there are special structures where the fore-gut and the mid-gut join. There is nearly always a muscular sphincter by which the contents of the two regions can be kept

separate ; and there is often a discrete organ known as the proventriculus. The proventriculus is a different morphological entity in different groups, sometimes being composed solely of fore-gut, while sometimes both fore-gut and mid-gut contribute to it. Its function also varies. In the Blattidae it is a powerful muscular organ or gizzard provided with rows of massive teeth, which seize and triturate the solid particles of food in the crop [79]. In many Hymenoptera it is a similar type of organ though with smaller teeth, but it has not been proved to have a grinding function [237]. In the flea it is lined with long needle-like teeth directed backwards; during digestion it contracts rhythmically, driving the teeth backwards into the mid-gut ; at the same time the mid-gut contents are driven up against it by anti-peristaltic waves, and in this way the blood corpuscles are pounded and disintegrated [288].

In most insects the fore-gut is invaginated to some extent into the mid-gut, and this invagination, surrounded by the anterior or cardiac region of the mid-gut, is also commonly referred to as the ' proventriculus '. The invaginated fore-gut is called the ' oesophageal valve ', though it seems never to function as a valve (if, by that word, is intended a mechanism which automatically allows movement in one direction only), for the occlusion of the passage between fore-gut and mid-gut is secured always by a sphincter muscle [280], and the invagination of the fore-gut has quite another significance.

The Peritrophic Membrane. The gut of insects contains no mucous glands ; the boluses and hard particles of food are therefore not lubricated as they are in the intestine of vertebrates ; and the epithelial cells obtain protection in another way. As was first observed by Lyonnet, they are separated from the gut contents by a delicate membrane, composed of chitin mixed perhaps with some protein [277], known as the peritrophic membrane. This membrane

is freely permeable to digestive enzymes and to the products of digestion; experimentally it has been shown to be permeable to all dyes save those with the largest colloidal particles [65]. In its primitive state the peritrophic membrane is a somewhat indefinite affair formed by the condensation over the surface of the food of certain constituents in the mid-gut secretion; and it arises in this way to a greater or less extent in many existing insects, where it is made up of a number of concentric layers, all of which are chitinous [65]. These membranes become separated from the general surface of the gut, but tend to remain attached at the anterior end, and are therefore apt to give a false impression of taking origin solely at this point. They remain attached in this region largely because here the mid-gut is overlaid by the oesophageal valve. That is probably the *raison d'être* of this invagination: it enables the peritrophic membrane to extend well beyond the point at which the food enters the mid-gut.

Now as the food passes through the oesophageal valve it will tend to press the walls outwards; and in so doing it will tend to press the secretion from the cells of this cardiac region into a membrane. That is the crudest form of mechanism by which the peritrophic membrane is pressed out; it is met with in the larvae of Lepidoptera [122, 280]. But in many insects the conditions have become far more elaborate. The cells in the cardiac region have become increasingly specialized for the production of the membrane until, in the Diptera and in the Dermaptera, they alone are concerned in its formation. At the same time the mechanisms by which the fluid secretion from these cells is pressed to form a solid tube become more complicated, until in many Diptera these annular moulds or presses present the most elegant forms [280]. Sometimes the oesophageal valve bears a rigid cuticular ring against which the cells of the mid-gut are forced (Fig. 8, A, C); sometimes the valve is

itself a solid structure made up of large vesicular cells (Fig. 8, B); sometimes, a rather cruder arrangement, the valve is thin-walled but contains blood sinuses which can be distended with fluid and so blown out against the cardiac cells.

The peritrophic membrane is present in the majority of insects. It has disappeared in the Hemiptera,

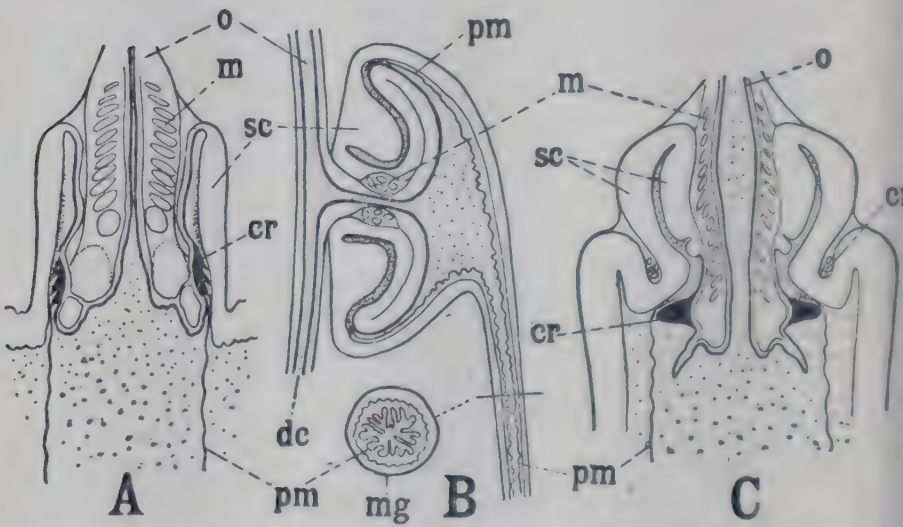

FIG. 8.—Annular moulds producing peritrophic membrane: A, larva of mosquito, *Anopheles*; B, tsetse fly, *Glossina*; C, earwig, *Forficula*. (Modified after Wigglesworth.) The cross-section of the membrane is equal to that of the mould in each case; hence the complicated folding of the membrane in the narrow part of the mid-gut in B.

cr, cuticular ring forming inner wall of press; *cm*, circular muscle compressing the outer wall against this ring; *dc*, duct of crop; *m*, sphincter muscle; *mg*, mid-gut; *o*, oesophagus; *pm*, peritrophic membrane; *sc*, cells secreting the substance of the membrane.

perhaps because these take only liquid food, and in various blood-sucking forms such as the Culicidae, Tabanidae, fleas and sucking lice; it is wanting also in the Carabidae and Dytiscidae, possibly because their digestion is largely extra-intestinal (see p. 50), possibly because their secretion is of the holocrine type (see p. 50) in which the secreting cells break

down completely during the process. It is absent also from adult ants [65].

Salivary Glands. Most insects possess salivary glands. Sometimes, as in the Apterygota [196] and in the bee [159], several kinds of glands, probably with very different functions, open in the region of the mouth; and even the single pair of labial glands present in most insects have very varied functions. (i) In the first place, their secretion may serve to moisten and dissolve the food: when a cockroach eats, its mouthparts are regularly moistened with saliva [276] and in the feeding butterfly a drop of saliva is extruded from the tip of the tongue [243]. (ii) Then their secretion often contains digestive enzymes which may act outside the body (as in the plant-sucking Aphids whose saliva dissolves the starch in the plant cells) [19] and which continue to act upon the food after it has been swallowed (amylase in the cockroach [247], invertase in butterflies [243] and bees [159]). (iii) In the Hemiptera, Diptera and Siphonaptera, which have mouthparts adapted for sucking up fluids, the saliva is discharged at the tip of the proboscis, and one of its functions may be to keep the tube, up which the fluids are sucked, moist and clean. (iv) And in those forms which suck the blood of living animals, the saliva usually contains an anticoagulin—probably antithrombin [58]. It has been shown that if the salivary glands are removed from the living tsetse fly, although it continues to take food for some time, ultimately its crop and proboscis become blocked with coagulated blood [176].

There is, however, much still to be learned about the salivary glands of insects. In many Hemiptera they consist of several lobes, which differ in histological structure and in the staining reactions of their secretion. What the functional significance of these differences may be is at present quite unknown.

It is interesting to note that many predaceous beetles (larvae of *Dytiscus*, *Carabus* and *Cicindela*,

and the adults of these forms) which lack salivary glands, as well as the ectoparasitic larvae of certain Hymenoptera, eject their intestinal secretion from the mouth, allow much of the digestion of their prey to take place outside the body, and then reabsorb the fluid products. This process is termed extra-intestinal digestion [174]. The flesh-eating maggots achieve the same result by discharging proteolytic enzymes in their excrement [127].

Secretion. The secretion of digestive juices in insects is commonly stated to be of two histological types : holocrine and merocrine. In the former type, which occurs notably in Orthoptera and Coleoptera, the active epithelial cells disintegrate completely in the process of secretion, and are replaced by the growth of new cells from special cell nests or nidi [234]. In the merocrine type, the cells do not break down. They may discharge their secretion, usually through a striated border, without any visible changes in the cell (save what may be detected by refined cytological methods) and that is probably the most common state of affairs. But a special type of merocrine secretion, known as vesicular secretion, is described, in which discrete droplets of fluid are eliminated through the striated border [44]. Unfortunately, identical droplets are only too easily produced artificially during fixation, and appear in abundance where during life they cannot be seen at all. But this does not, of course, exclude the possibility that in some cases vesicular secretion may actually take place. Sometimes the cells of the gut contain conspicuous vacuoles, and these are often taken as evidence of secretory activity. But it must not be forgotten that such vacuoles may equally well arise in the course of absorption [45]. In Aphides, fed after a period of fasting, successive waves of secretory activity appear to pass down the stomach [268].

The Reaction of the Gut. As was discovered long ago by Plateau, the intestinal contents of insects

are not as a rule strongly acid or alkaline. The saliva in those forms in which it has been examined is usually neutral [276, 277]; the gut contents usually slightly acid, having a *p*H between 6 and 7 [163]. The contents of the gut tend, on the whole, to be more alkaline in phytophagous insects (*p*H 8·4–9·0 in some herbivorous Coleoptera, *p*H 8·4–10·3 in the silkworm [235]) and more acid in carnivores [19]; but there are many exceptions [163]. Well-marked acidity (*p*H 4·8–5·2) may develop in the crop of the cockroach, after a meal of carbohydrates, as the result of acid fermentation by micro-organisms [276]; and sometimes the insect itself is responsible for a quite strongly acid secretion; as in a well-defined region in the intestine of the blowfly maggot, which has a *p*H of 3·0–3·5, the acidity being due probably to phosphoric acid [127].

Digestive Enzymes. The digestive enzymes of insects are such as might be predicted from the nature of their food. Omnivorous forms, like the cockroach, have a full complement of enzymes capable of digesting all the common foodstuffs.[247] Insects which take chiefly a protein diet, such as the exclusively blood-sucking species, have little but proteolytic enzymes.[277] Where an insect feeds only on nectar, as in the adults of Lepidoptera, only an invertase is present [243]; whereas the phytophagous larvae of these same forms have a protease, lipase, amylase, maltase and invertase [243]. A few examples to illustrate this general relation between the nature of the food and the enzymes present, are given in Table I; many more such examples could be quoted. It will be seen that most of the enzymes are secreted in the mid-gut; the salivary glands rarely secrete anything but amylase, and often contain no enzymes at all.

These enzymes are readily demonstrated in extracts from the gut. They are present also in the juice removed from the lumen [247], showing that at least the greater part of digestion is extracellular. Sometimes attempts have been made to demonstrate the

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existence of enzymes by observing the time of survival of insects upon pure foodstuffs [259]. Such experiments may throw valuable light upon the significance of particular substances in nutrition [264], but they cannot, of course, prove the existence of enzymes; for positive results may be due to absorption without hydrolysis, or to bacterial fermentation.

The properties of the enzymes of insects are, in general, very like those of the corresponding enzymes from vertebrates [276]. They are similarly affected by changes in hydrogen ion concentration, and are stimulated or inhibited by the same factors. The chief proteolytic enzyme seems always to be more or less like pancreatic trypsin,* though it often acts best over a rather more acid range of *p*H [127, 277]. Enzymes of the pepsin type acting in very acid media do not occur. Certain special enzymes are present in those insects which feed on particular substances; for instance, the meat-eating maggot (*Lucilia*) has a collagenase which attacks raw connective tissue in alkaline medium [127]; and a few of the wood-boring beetles produce a cellulase [219]. (The clothes moth (*Tineola*) can digest keratin, and the bee moth (*Galleria*) can digest wax—in both cases probably without the aid of bacteria—but active preparations of the enzymes concerned have not been obtained [163].)

So many insects feed on the foliage and woody tissues of plants that particular interest attaches to the question of cellulose digestion. In the vast majority of species, the cellulose is quite unaffected by passage through the intestinal canal: those plant cells that are not ruptured by the jaws of the caterpillar pass through the gut with their walls intact, although their contents may be digested [20]; the excrement of many wood-boring beetles contains all the lignin and cellulose that have been ingested with

* The proteolytic enzymes of insects have not yet been studied on modern lines with the object of differentiating their trypsin into its constituent elements.

TABLE I

Insect	*Food*	*Enzymes*	
		Salivary Glands	*Mid-gut*
ORTHOPTERA			
Cockroach (*Periplaneta americana*) [276]	Omnivorous	Amylase	Amylase ; maltase ; invertase ; lactase (in very small amounts) ; tryptase ; peptidase ; lipase.
COLEOPTERA			
Japanese beetle (*Popillia japonica*) [243]	Foliage	—	Maltase ; invertase ; tryptase ; lipase.
HYMENOPTERA			
Honey-bee (*Apis mellifica*) [85, 159]	Nectar and pollen	Amylase ; invertase	Amylase ; invertase; tryptase ; lipase.
LEPIDOPTERA			
Silkworm (*Bombyx mori*) Larva [235]	Foliage	—	Amylase ; maltase ; invertase (chiefly in the cells) ; tryptase ; peptidase (only in the cells) ; lipase (in very small amounts).
Humming bird hawk moth (*Macroglossa stellatarum*) Adult [243]	Nectar	Invertase	Invertase.
DIPTERA			
Blowfly (*Lucilia sericata*) Larva [127]	Flesh	Amylase (very weak)	Tryptase ; collagenase ; peptidase ; lipase.
Blowfly (*Calliphora*) Adult [277]	Liquid food of all kinds	Amylase	Amylase ; maltase ; invertase ; weak tryptase and peptidase.
Chrysops silacea Adult [281]	Female : blood. Male : nectar, &c.	Nil.	Very weak amylase; strong invertase ; tryptase ; peptidase.
Tsetse-fly (*Glossina*) [277]	Blood	Nil.	Very weak amylase; strong tryptase ; peptidase.

the food [163]; the very starch grains may be protected from digestion by their pectin covering. On the other hand, many insects can digest cellulose; sometimes by means of cellulase they secrete themselves [219], sometimes with the help of symbiotic micro-organisms.

Symbionts in Digestion. Many insects have a rich fauna of bacteria or protozoa in the gut, but in none is this so prominent as in the hind-gut of wood-boring termites. Here there is an amazing population of flagellates, ciliates and spirochaetes, which perform for their host the invaluable function of digesting cellulose [56]. Termites with this fauna intact can thrive indefinitely upon pure cellulose; but if the insect is deprived of these organisms (by exposing it to a high tension of oxygen, for example) its powers of digesting cellulose are completely lost, and unless reinfected it soon dies [56]. Cellulase can be extracted from the flagellates in the gut of these termites and of certain cockroaches (*Cryptocercus*); whereas this enzyme is absent from defaunated insects [257].

Certain Lamellicorn beetle larvae (*Cetonia*, *Oryctes*, *Osmoderma*) that feed on pine-needles and such like, ingest with their food those micro-organisms which ordinarily ferment cellulose in nature. These flourish in the dilated hind intestine (the so-called 'fermentation chamber') of these larvae, and form an important, perhaps an essential, aid to digestion [270]—being themselves digested later by the proteolytic enzymes of their host [273]. The same occurs in some Tipulid larvae [46]. But there are related beetles (*Dorcus*) which have a similar fauna and yet are said not to digest cellulose [219]. Other insects that feed on wood harbour yeast-like organisms, often within the cells of the gut; and it was natural to attribute to these, also, the function of digesting cellulose. But, in fact, some beetles that have such 'symbionts' are unable to digest cellulose, and others which are without them can do so [163]. Many blood-sucking insects, also, possess intracellular bacteria or yeasts in their tissues;

and the occurrence of these in close association with the gut, in the case of the tsetse-fly (*Glossina*) and the Pupipara, led to the suggestion that they were concerned in the digestion of blood [46]. On the face of it this was not a probable hypothesis, for the blood proteins do not differ specially from those of other tissues ; and it has been shown (at least in the tsetse-fly) to be incorrect ; for no digestion of the blood takes place in that anterior part of the mid-gut in which the symbionts occur [277]. If they are true symbionts, these organisms must have some other function (p. 72).

Absorption. In the cockroach, in which the food is digested largely in the crop, a small amount of absorption, notably of fats, may also occur in that segment of the fore-gut [1] ; but the greater part of absorption undoubtedly takes place in the mid-gut. The cells seem never to take up solid particles ; the dissolved foodstuffs, like the digestive enzymes, diffuse through the peritrophic membrane, when such is present, and are absorbed by the epithelial cells. In the blood-sucking insects, such as the tsetse-fly or the mosquito, almost nothing is passed on to the hind-gut, save a little haematin [284]. In these forms the hind-gut clearly plays no part in absorbing foodstuffs ; but whether this is generally true is uncertain. We have seen that the greater part of digestion in wood-eating termites and Lamellicorns takes place in the hind-gut ; to what extent the products are absorbed here, or returned to the mid-gut, is not known ; but the hind-gut of Lamellicorn larvae has special areas of cells which are believed to be concerned with absorption [273]. Water is certainly absorbed in the hind-gut and rectum of many insects (p. 65) ; and the food residue, in contact with the rectal glands, may be converted to a more or less dry faecal pellet [284] ; but whether other substances, also, are absorbed has not been satisfactorily demonstrated [243].

CHAPTER V

EXCRETION

THE function of the excretory organs of animals is to maintain a more or less constant 'internal environment'. To this end they may be called upon to eliminate several classes of substances: (i) substances, like mineral salts or water, which are present in simple excess in the diet; (ii) the end products in the metabolism of organic nitrogen, sulphur and phosphorus, of which, particularly of nitrogen, there is always a large surplus for excretion—these form perhaps the most important category of excretory substances; (iii) more or less complex compounds, not uncommonly pigmented, which arise perhaps as accidents or by-products in the course of other chemical changes, and which have to be excreted because the chemical equipment of the body is powerless to deal with them; (iv) and, finally, in order to maintain such properties of the blood as the hydrogen ion concentration, or the osmotic pressure, the excretory organs may be called upon to remove certain substances such as acids or bases, or to hold back others such as water.

Excretion of Dyes. Organs may fairly be regarded as excretory if they perform these functions, or eliminate one or more of these classes of substances. But, in practice, it is not always easy to recognize these activities; and therefore a second, experimental, criterion of excretory organs has come to be used—the excretion of dyes introduced into the body. This test must be used with discretion; for different dyes

re absorbed by different tissues: methylene blue, or example, is taken up by the nervous system, by he tracheal cells and by the oenocytes, and is there- ore of no use for this purpose [133]. The most reliable lye is indigocarmine, which seems to be removed pecifically by the excretory organs of all animals. When indigocarmine is injected into insects, it rapidly ppears in the Malpighian tubes, which are un- questionably excretory organs [78]. In the primitive Apterygota it appears, also, in the lower segment or abyrinth of the labial glands [42], and it is probably orrect to regard these also as excretory organs, omologous perhaps with the excretory glands of Crustacea. That is all the information obtainable with indigocarmine.

But if the acid dye ammonia carmine (which, in ertebrates, is filtered through the glomerulus of the renal tubule) is injected into insects, it is not excreted by the Malpighian tubes, but is absorbed and segre- gated by special cells—notably, by the 'pericardial cells' which lie along the dorsal heart and aliform muscles [62], by the 'garland-like strand' discovered by Weismann in the Muscid larvae, by various scattered groups of cells [43], and, in the Apterygota, by the upper segment or saccule of the labial gland [42]. On this evidence Kowalevsky put forward the view hat these cells are excretory organs (so-called 'acid excretory organs', because litmus is turned red within hem) analogous in function to the kidney glomerulus.

'Nephrocytes.' Kowalevsky's experiments were so striking that this theory at once gained acceptance; but it is doubtful if it will bear close examination. Our ideas on the kidney glomerulus have changed so much in the last forty years that Kowalevsky's analogy carries no weight at all. If the ammonia carmine cells are really 'storage kidneys' (nephro- cytes, athrocytes) as the theory implies, the waste substance which they accumulate during life should at least be visible. But in many insects nothing

seems to accumulate within them at all [62, 136]. Often they contain pigmented granules [136]; but this is the case with many cells—in the fat body, epidermis, tracheal matrix and so forth. Occasionally, they may become laden with some pigment from the food [147]; and it cannot be denied that they are then serving as 'storage kidneys' for this particular substance; but this can scarcely be their chief function. Perhaps they play some undetermined part in intermediary metabolism [136]; or they may be excretory organs in the sense of synthesizing the waste products that are to be eliminated by the Malpighian tubes [62]. They are highly capricious in their absorptive properties: they will take up various proteins; they will absorb some dyes, but not others; and it has not been possible to recognize any common feature in molecular structure or physical or electrical properties to account for these differences [136]. But these properties are very doubtful evidence of an excretory function; for, in vertebrates, similar properties are shown by the reticulo-endothelial system and by the connective tissue fibroblasts.

Urate Cells. As was observed by Milne Edwards and later by Fabre, there are cells in the insect body which become laden with crystalline spheres of uric acid ('urate cells'); and they surely can be regarded as storage kidneys, for uric acid is an undoubted excretory substance. In many cases this view is probably correct; throughout larval life in the social Hymenoptera, uric acid collects in solid form in special urate cells scattered throughout the fat body [229], and is not transferred to the Malpighian tubes (of the adult) until the end of pupal life; in *Lepisma*, Dermaptera and many Orthoptera, this state of affairs persists throughout life, and the Malpighian tubes discharge very little uric acid [284]. But even here the observations must be interpreted with caution. For uric acid is the end product of protein katabolism; and when protein breakdown is occur-

ing very actively within a cell, it is likely that the rate of formation of uric acid may, on occasion, exceed the rapidity with which it can diffuse from the cell and be carried away by the blood; particularly if conditions in the cell become unduly acid. The uric acid will then crystallize out, and its subsequent solution and removal will take place very slowly. That indeed is what appears to happen in the cells of the fat body in Muscidae during metamorphosis: granules of uric acid ('pseudonuclei') crystallize out within the 'albuminoid' deposits, and not until late in pupal life is the uric acid transferred to the Malpighian tubes [208]. The same thing happens in Lepidoptera; and here the uric acid must be endogenous, for it is not increased by the artificial introduction of preformed uric acid [134].

It is probable that not a few of the urate cells of insects are of this nature—not true excretory organs but active cells in which uric acid has crystallized out, as it were, by accident. For instance, the epidermal cells of some Hemiptera contain uric acid; but it has been shown that in one case at least, that of *Rhodnius prolixus*, the deposition of this uric acid takes place only at one stage of the moulting cycle—just before the new cuticle is laid down; that is, when the cells in question are most active in producing chitin—perhaps from the proteins of the food [286].

Pigments. Now besides this uric acid, there is in the epidermal cells of *Rhodnius* a red pigment, which appears at the same time as the uric acid, and then slowly diminishes [286]. Perhaps this substance, also, is a by-product of the synthetic activity of these cells; and perhaps that is the origin of many of the pigments of insects—accidents in metabolism, which only secondarily acquire their biological significance. Certainly this is the case with the pigments of the Pieridae; as was shown by Hopkins [130] many years ago, these are composed of uric acid and complex

derivatives of uric acid [274] which, instead of being transferred from the fat body to the Malpighian tubes, are deposited in the scales of the wings [275]. The same applies perhaps to the red pigment of Vanessid butterflies; though this is not related chemically to uric acid [191].

Verson's Glands. It has been observed that when the silkworm casts its skin, its body may be powdered with crystals of oxalate and uric acid derived from the moulting fluid; and this led to the suggestion that, at the time of moulting, the Malpighian tubes are thrown temporarily out of action, and their excretory function taken over by the moulting glands (Verson's glands) [263]. But this idea has been shown to be mistaken; the excretory substances in the moulting fluid really come from the Malpighian tubes, escape through the anus beneath the old cuticle, and so spread over the surface of the body [233]. (It is just possible that the calcareous warts of Stratiomyid larvae (p. 3) may also be formed in this way. On the other hand, the lime which appears in the ecdysial fluid of certain Diptera at the time of pupation is said to be dissolved from the Malpighian tubes, reabsorbed into the blood, and excreted through the newly-formed cuticle [146].)

The Malpighian Tubes and the Urine. When all these subsidiary processes have been considered, the Malpighian tubes still remain unquestionably the chief excretory organs. The Malpighian tubes are relatively simple tubular glands which open at the junction between the mid-gut and the hind-gut. They are exceedingly variable in form [269]: sometimes being numerous (e.g. over 100) and short, sometimes few in number (e.g. 2) and long; sometimes simple and sometimes branched; occasionally anastomosing to form closed loops; while sometimes more than one type of tube is present [78]. Their histological structure is no less variable. Usually their epithelial cells bear a striated border, but this may

be wanting; sometimes this border is of the type known as 'Wabensaum' in which the rod-like elements are fused together; sometimes it is made up of separate mobile filaments ('Burstensaum' [283]). Sometimes the tubes have a muscular coat and are capable of active movements; more often they show only slow twisting movements due to changes in the secretory pressure within them [78]. Many histological changes have been described in the active cells of the Malpighian tubes: the discharge of vesicles, the eruption of vacuoles, and so forth. It is not improbable that more than one cytological mechanism of excretion may exist; but certainly many of the recorded observations are artefacts [283].

The urine which the Malpighian tubes secrete is equally varied. It may be a clear fluid or a thick pasty suspension: the colourless fluid passed by blood-sucking insects soon after a meal is an example of the former sort, the 'meconium' of newly emerged Lepidoptera of the latter. Its constituents depend naturally upon the nature of the food, but it always consists primarily of water with the usual inorganic salts, chlorides and phosphates of sodium, potassium, calcium and magnesium, in solution. Yellowish or greenish pigments ('entomo-urochrome') are often present; but it is likely that these differ chemically in different species [78]. Nitrogen is excreted chiefly as uric acid; but urea has been reported in substantial amounts in the urine of the clothes moth [283], and meat-eating maggots are said to eliminate much of their nitrogen as ammonia [127]. The amino acid leucine has been recorded by many earlier authors, but the evidence rests only on crystal structure and requires chemical confirmation [78]. Guanine, the main nitrogenous constituent in the urine of many Arthropods, seems not to occur in insects; but the nitrogen compounds of insect urine are still very incompletely studied. The reaction of the urine naturally varies with the diet, and the period after feeding; the thick

meconium of Lepidoptera has a *p*H of 5·8–6·3 [120]; the similar urine of the bug *Rhodnius prolixus*, shows the same kind of range [283].

When uric acid is present in the urine it is usually in the form of crystalline spheres with a radial striation. These spheres are commonly stated to consist of ammonium acid urate, or of sodium or potassium acid urate; but in *Rhodnius*, almost the only insect in which this question has been investigated chemically, they consist mainly of free uric acid [283]; and it is possible that this is also the case in other insects.

Beside these crystals of uric acid, the Malpighian tubes may contain solid spheres or granules of calcium or magnesium carbonate [75, 205] and, notably in the larvae of Lepidoptera, crystals of calcium oxalate [78]. The oxalate is possibly derived from the preformed oxalic acid in the food, but the significance of the accumulated carbonates is uncertain. They are sometimes used by the pupating larva to strengthen its cocoon (Cerambycidae, Col.) or its puparium (Agromyzidae, Dipt. [146]), or by the female to calcify the shells of her eggs (Phasmidae, Orth. [205]), but these are probably secondary adaptations. It has been suggested that the carbonates may constitute a method of eliminating carbon dioxide [146]; but such a mechanism seems uncalled for, and in any case the amount of carbon dioxide bound in this way must form but a fraction of what the insect produces. Perhaps these carbonates simply provide a mechanism for getting rid of excess alkali; it is at least noteworthy that they occur chiefly in saprophagous and phytophagous larvae of Diptera (Stratiomyiidae, Drosophilidae, Agromyzidae and many more) whose food might be expected to contain an excess of fixed base. Their urine must therefore be alkaline, and in the presence of the carbon dioxide of the tissues, if calcium or magnesium ions are present in quantity, carbonates will tend to precipitate. It is worth noting that carbonates are present in the phyto-

phagous Agromyzid *Acidia*, but not in the parasitic genus *Cryptochaetum* [251]; and they are said to be absent in aquatic larvae from very acid waters [165]. (It may be noted in passing that similar deposits of lime ('calcospherites') may occur in the fat body of some insects [146].)

Excretion in Rhodnius. Now insects are essentially terrestrial animals. Consequently, the main problem with which their excretory system is faced is the elimination of all these substances, and particularly the elimination of nitrogen, in such a way that they are able to conserve their limited supplies of water. And it is instructive to consider the excretory system from this point of view. It will be convenient to start by describing the excretory system of the blood-sucking bug *Rhodnius prolixus*, which has been studied in considerable detail [283], and then to compare with this some other insects.

The excretory system of *Rhodnius* consists of four very long Malpighian tubes, opening into a large rectal sac (Fig. 9, A). Each tube is made up of two distinct segments: a translucent upper segment, about two-thirds of the whole, the lumen of which contains only a clear fluid, and an opaque white lower segment stuffed with spheres of uric acid. The histological structure of these two segments is quite different; the one changes abruptly into the other; and immediately below the junction the granules of uric acid appear in the lumen (Fig. 9, B). The explanation of these facts which has been suggested is that the upper segment of the Malpighian tube is secreting a solution of sodium or potassium acid urate, and the lower segment reabsorbing both the water and a large proportion of the base (sodium or potassium—perhaps in the form of bicarbonate) leading to a precipitation of the free uric acid. For it can be shown (i) that the contents of the upper segment (pH = 7·2) are definitely more alkaline than those of the lower segment (pH = 6·6); (ii) that

neutral red added to the blood of the insect is secreted into the lumen by the cells of the upper segment and reabsorbed again by the cells of the lower segment; and (iii) that if two ligatures are applied to the tube near its lower end at a time when the uric acid spheres have been washed out by a recent meal, then uric acid

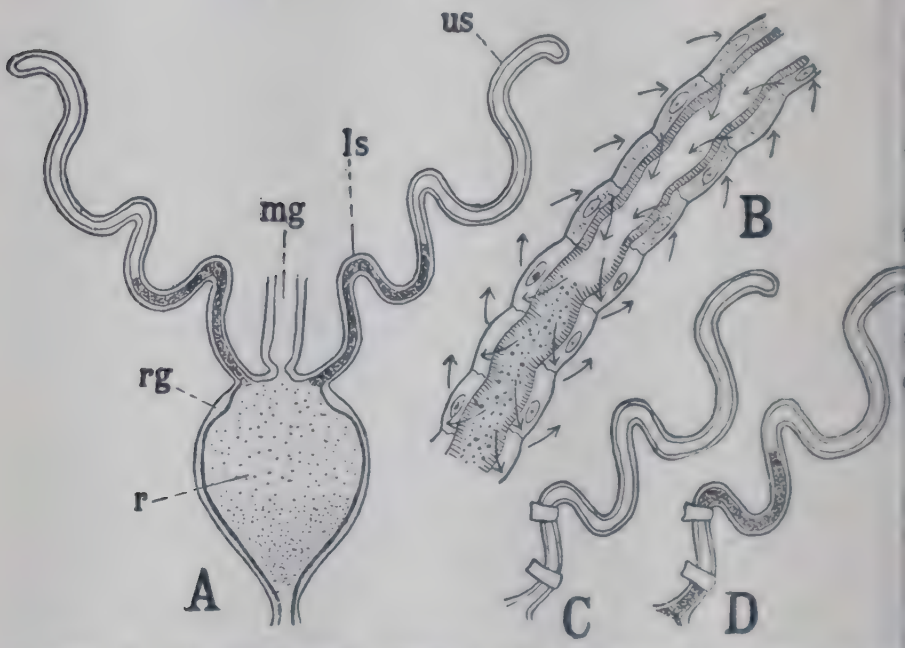

FIG. 9.—A, excretory system of *Rhodnius*: schematic; B, detail of Malpighian tubes at junction of upper and lower segments; arrows indicate the circulation of water and base; C, two ligatures applied to Malpighian tube three hours after meal; D, the same 24 hours later. (Modified after Wigglesworth.)

ls, lower segment of Malpighian tube: lumen full of uric acid spheres; *mg*, mid-gut; *r*, rectum; *rg*, rectal gland; *us*, upper segment of tube.

appears above the upper ligature and below* the lower ligature, but between the ligatures there is no uric acid, nor is there any distension of the tube (Fig. 9, C, D).

Thus it is suggested that, in *Rhodnius*, there is a

* This has doubtless been derived from the other Malpighian tubes, and has entered from below.

continuous circulation through the excretory system both of water and of base, the same water and base being used over and over again to carry uric acid from the body.

It is not unlikely that the rectum, also, assists in the process of reabsorbing water; for around the point of entry of the Malpighian tubes there is a ring of large epithelial cells constituting a so-called rectal gland; and we shall find that there is evidence in other insects that the function of the rectal glands is the absorption of water from the excrement.

Excretion in Other Insects. This conception of a circulation of water through the excretory system is a familiar one in the physiology of birds, and reptiles, and mammals, where the renal tubule itself, the cloaca, and the large bowel all take part in the reabsorption of water. It is an idea that has only recently been introduced into the physiology of insects [284]; but it helps to explain many of the properties of their excretory system.

The simplest system that occurs is that shown in Fig. 10, A. Here the Malpighian tubes are composed of a single type of cell, and contain only fluid. As this fluid, mixed with the intestinal contents, passes down the hind-gut, water is absorbed from it—first by the cubical epithelium of the intestine and finally by the epithelium of the rectum. The material is retained in the rectum until it has been converted into a more or less dry pellet. In some cases, for instance in the human louse *Pediculus*, the contents of the mid-gut may be retained in the stomach so that the hind-gut contains only urine; under these circumstances, a little pellet of solid uric acid may be formed in the region of the rectal glands, clearly demonstrating the absorption of water by these organs [284]. This arrangement is found in *Lepisma*, Dermaptera, Orthoptera, Neuroptera, and many beetles. In some cases the active epithelial cells of the rectum are collected into compact areas, the

'rectal glands'; in other cases they are evenly spread over the gut wall.

In many beetles, phytophagous, carnivorous and omnivorous species [183], as well as those that feed on

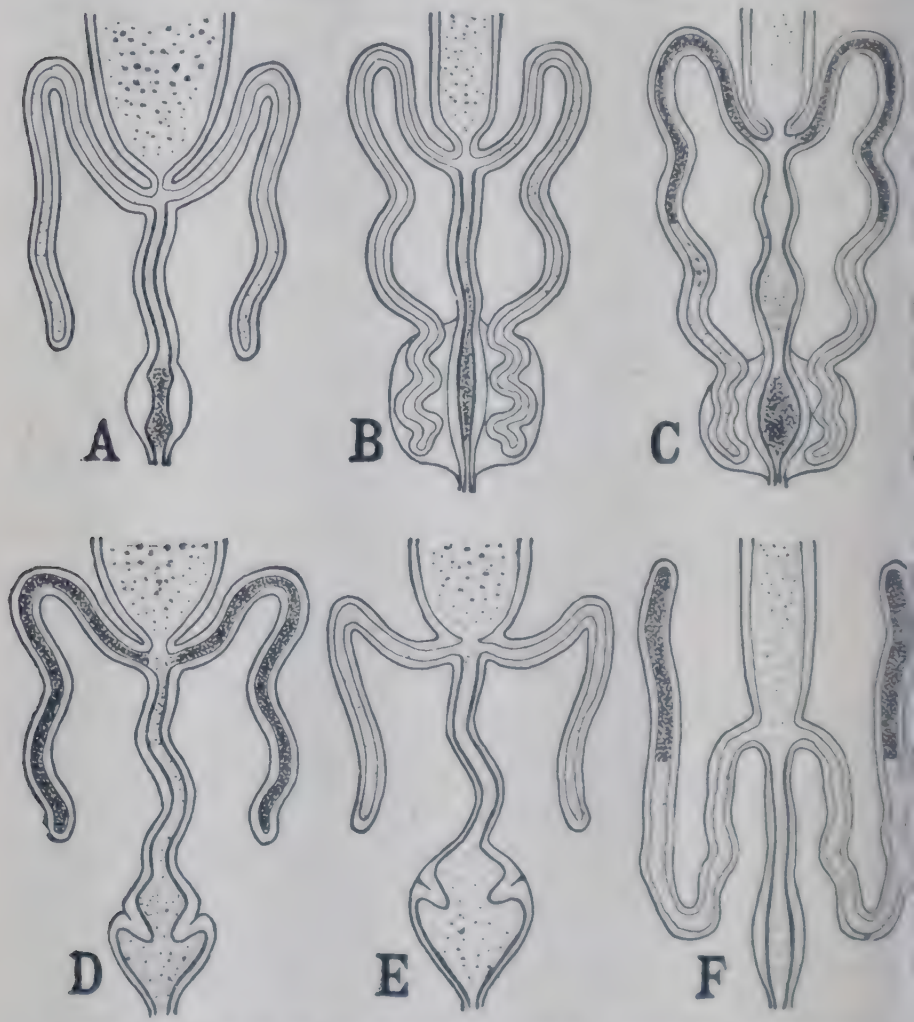

FIG. 10.—Types of excretory system in insects: schematic Hind-gut indicated by a heavy line internally. Explanation in text.

dry substances [210], such as the mealworm (*Tenebrio*), the upper parts of the Malpighian tubes closely invest the rectum, being bound to it by a delicate membrane (Fig. 10, B). The precise significance of this arrange-

ment is not known; perhaps it serves to add the absorptive powers of the Malpighian tubes to those of the rectal epithelium; but the arrangement seems always to be associated with remarkable powers of drying the excrement. The rectum of the mealworm, for instance, contains a bone-dry powder, consisting largely of uric acid, while the Malpighian tubes secrete only a clear fluid [284].

A similar arrangement is met with in the larvae of Lepidoptera (Fig. 10, C) [143]. But here the lower part of each Malpighian tube contains solid granules of uric acid, oxalate, &c. [78]; and this suggests that, as in *Rhodnius*, the Malpighian tubes themselves assist in reabsorbing water.

In many Diptera (the mosquito, Muscid flies, &c.), the Malpighian tubes may contain solid uric acid throughout their length (Fig. 10, D) [284]. The tubes consist apparently of but a single type of cell, so that the mechanism for the precipitation of uric acid must be different from that in *Rhodnius*. In the rectum, a further absorption of water probably occurs; but these insects lack the power of really drying the excrement. Conditions are somewhat similar in certain Hymenoptera. In other Hymenoptera, the excretory system is like that of the flea (Fig. 10, E). It never contains any solid uric acid because sufficient water is retained in the capacious rectum to keep it in solution; but it is none the less probable that this fluid is reabsorbed, and circulates again through the system [284].

Finally, in those many dipterous larvae in which the Malpighian tubes contain carbonates, these are generally confined to the upper part of the tube (Fig. 10, F); but the mechanism of their secretion is unknown [75, 205].

These are just a few of the arrangements of the Malpighian tubes and hind-gut, which will serve to illustrate the general principles of excretion in insects so far as these are known at present; many other

arrangements exist. And it should be pointed out that many other hypotheses as to the function of the rectal glands of insects have been put forward from time to time [284]. Some of these are certainly incorrect; but others are probably subsidiary functions in particular species.

Excretion in Aquatic Insects. Lastly, it is interesting to consider what changes take place in the excretory system of insects when they come to live in fresh water, and are no longer compelled to be so careful of their water supply. This matter has received little attention; but in the case of the mosquito larva, there is around the anus a group of hollow papillae, the so-called 'anal gills'. These are covered with chitin, but with chitin devoid of its cuticulin coat and therefore, unlike the rest of the body surface, freely permeable to water. In superficial appearance these organs look strikingly like rectal glands that have prolapsed through the anus; and indeed it has been shown that they also are engaged in absorbing water, not from the excrement but from the environment [285]. This water is excreted by the Malpighian tubes, which are kept so well flushed out that normally they never contain any solid uric acid. But if the larvae are reared in isotonic or slightly hypertonic salt water, in which absorption no longer takes place, masses of solid granules frequently make their appearance in the lumen of the Malpighian tubes [285].

Accessory Functions of the Malpighian Tubes. Réaumur observed that the lemon yellow powder used by the larva of *Malacosoma neustria* to cover its cocoon is a product of the Malpighian tubes. Such products are used by other Lepidoptera: *Leucoma salicis*, *Eriogaster lanestris* and so forth [64]; and we have already seen how Cerambycidae strengthen their cells with lime from this same source. The foam or cuckoo-spit produced by the larvae of Cercopidae is formed from the Malpighian excretion mixed with

the product of some other glands [268]. And in the larvae of such widely separated insects as *Lebia* (Carabidae) and certain Neuroptera, a portion of the Malpighian tube is transformed into a silk gland [64].

CHAPTER VI

NUTRITION AND METABOLISM

SINCE the alimentary canal of insects contains digestive enzymes competent to hydrolyse those constituents commonly present in their food (p. 51), it is probable that this food is absorbed in the form of simple products of hydrolysis : carbohydrates as monosaccharides, fats as glycerol and fatty acids, protein as amino acids. But at present there is no proof of this, and it is possible that there may be some absorption of more complex bodies. Little is known, either, of the fate of the absorbed products. Presumably, the tissue cells take from the blood what they require for growth, energy production or secretion ; and surplus food is certainly taken up by the cells of the fat body, in which it is stored as glycogen, fat and protein. But what is quite unknown is where the intermediary stages of metabolism take place. If amino acids are condensed to form protein before storage, where is this done ? Where is carbohydrate converted into fat ? When unwanted proteins or amino acids are deaminated, is this effected by those tissue cells which require the products, or by some organ specially devoted to this branch of metabolism ?

It is possible, though no very certain evidence of this yet exists, that the pericardial cells may be responsible for some of these activities (p. 57) [136] ; and it has been suggested that the oenocytes may be concerned either in some general process of intermediary metabolism [133, 160], or in the special process of synthesizing certain constituents of the cuticle [286]. On

the other hand, the accumulation of solid uric acid in the fat body when protein reserves are broken down (p. 58), and in certain cells of the cuticle during moulting (p. 59), suggests that the powers of deamination and uric acid formation are shared by many tissues; though the chemical details of both these processes are unknown.

Food Requirements. We have seen how exceedingly varied are the apparent food materials of insects (p. 42). But it must be remembered that insects are not always feeding upon what they eat: they may devour rotten wood but feed only upon the fungi which it harbours; or eat large quantities of cellulose and yet assimilate only the associated substances [259].

The principles of insect nutrition are therefore not easy to state. It is self-evident, though it is sometimes forgotten by writers on the subject, that for growth and reproduction, insects must have an adequate supply of carbon, and nitrogen, phosphorus and sulphur, inorganic salts and all the other elements that go to make up the living system. There is, at present, little information as to what may be the simplest substances which will satisfy these needs in a given insect; but there is certainly no reason to suppose that they are any simpler than those required by vertebrates. *Drosophila* has been reared with ammonium salts [259], and cockroaches with glycine [296] as the sole source of nitrogen; but these insects have in the intestine a notoriously rich flora of yeasts and bacteria which may well have been responsible for essential syntheses. For the maintenance of life and activity, on the other hand, without growth, insects can subsist for long periods on carbohydrates alone [296], and Lepidoptera usually live only on sugars throughout their adult life. The hexose monosaccharides which can or cannot be metabolized under these circumstances are much the same as those in other animals, but (for the bee at any rate) the pentoses seem to have no food value [264]. There are much

wider differences in respect to the di- and tri-saccharides, due no doubt to the presence or absence of appropriate enzymes [264].

Vitamins and Symbiotic Organisms. One aspect of nutrition that has been explored considerably is that relating to accessory substances or vitamins [259], and the part played by micro-organisms in providing these. The larvae of the blowfly *Lucilia* can be grown from sterile eggs on the sterile brain of mammals; they will not grow on certain types of sterile muscle. But if the muscle is infected with suitable micro-organisms, or if a sterile extract of yeast is added to it, normal growth is obtained. The bacteria and the yeast provide a vitamin (belonging to the B group of vitamins) that is present in brain but lacking in muscle [128]. It is interesting to note that sterile blood, also, is an insufficient diet for these larvae; it can be rendered adequate by the addition of vitamin B_1 [128]. Now many insects (the bed-bug (*Cimex*), the sucking lice, the tsetse-fly (*Glossina*), the Pupipara) take no food throughout their life except sterile blood. But all these insects * contain within their bodies special groups of cells (mycetomes) stuffed with supposedly symbiotic micro-organisms [46], which are absent from such insects as mosquitoes, fleas, &c., that take blood during part only of their life cycle. This naturally suggests that these symbionts may constitute an endogenous source of vitamin, and thus enable these insects to grow on sterile blood [6, 277]; indeed, it has been shown experimentally that if the louse *Pediculus* is deprived of its mycetome and symbionts, its powers of nutrition and reproduction are greatly impaired, and that this impairment may be made good, to some extent at least, by the addition of yeast extract to the diet [7].

* The blood-sucking Reduviidae (*Rhodnius*, *Triatoma*, &c.) are an exception, and have no intracellular symbionts. But they regularly have the gut contents heavily infected with a diphtheroid bacillus or a streptothrix, the source of which has not yet been determined [288].

Fat soluble accessory substances, more or less related to vitamin A, are perhaps also required by insects [217, 246]; vitamin C seems not to be necessary [246]; but some insects apparently need factors differing from those known in vertebrate nutrition [128]. It is clear, therefore, that when insects feed upon a sterile and restricted diet, the supply of vitamins may become a problem of some urgency; and it is possible that the association of sterile food (as in the majority of plant-sucking Hemiptera) with the presence of symbionts, may again be traced to this need. But at present there is no experimental proof of this, and difficulties are presented by the occurrence of symbionts in the omnivorous cockroach, and their presence in some wood-boring insects (p. 54) but not in all [46]. The same difficulty, of course, is encountered in any of the suggested hypotheses of symbiotic function: whether the symbionts are digesting cellulose [46], fixing atmospheric nitrogen [117], or synthesizing vitamins, it is not easy to see why related forms (Cerambycid larvae, for example), with and without symbionts, should grow with equal rapidity on the same diet [219]. But the insect and its symbionts show such wonderful mutual adaptations, that it is equally difficult to dismiss the whole phenomenon as one of harmless parasitism.

Water Metabolism. Another fundamental requirement in insect nutrition, and a very important one, is water. Even such an insect as the weevil *Calandra*, which is accustomed to feed in dry materials and is highly adapted to conserve the water in its body, cannot survive unless its food contains some 10 per cent. of water [142]. In other words, the water produced from the oxidation of foodstuffs, although of great importance to the insect, is not, alone, sufficient for its needs. If the mealworm is kept in air with a relative humidity of 90 or 95 per cent., it is able, by some mechanism that is quite unexplained, to absorb water from the atmosphere [185]; but this

property is very unusual; most insects cannot absorb water vapour even when the air is saturated [52, 57]. On the other hand, the *loss* of water (when this occurs by evaporation as opposed to excretion (p. 56)) is markedly affected by the water vapour in the air. The rate of loss, like that from inanimate bodies, has been found, within certain limits, to be more or less proportional to the saturation deficiency of the air [52]. It is not, of course, to be expected that such a law should hold very exactly, especially at varying temperatures, because evaporation occurs chiefly from the tracheal system [109, 188], the ventilation of which varies with the intensity of metabolism in the insect and so with the external temperature (p. 21) [115].

But apart from the importance of water as a constituent of the tissues, it plays a significant part in the reaction of the insect to extremes of temperature in its environment. When exposed to high temperatures, an insect may be killed (depending upon the conditions of experiment) by the temperature itself or by the desiccation consequent upon evaporation [186]. Now, provided the insect in question is sufficiently large, it will be able to lower its temperature below the fatal level (for short periods at any rate) by evaporating water from its body, and thus to exercise a limited degree of temperature control [186]. And it has been found that insects which have lost a certain amount of water by desiccation are, for some unknown reason, more resistant to high temperatures. Normal individuals of *Leptinotarsa* die at 58°–60° C., desiccated ones at 1°–5° higher [52]. The same loss of water also makes them more resistant to low temperatures [142]: if the larva of the beetle *Popillia japonica* is experimentally dehydrated to half its body weight, it becomes exceedingly resistant to cold, and can survive exposure to −28° C. [207]. In association perhaps with this phenomenon, it is usual for insects to reduce their water content before going into hibernation; this reduction is certainly one factor in

the increased resistance of insects to cold during the winter [207]. When the water content is reduced in this way, the freezing point and undercooling point (the lower limit of supercooling) of the whole insect are lowered—partly perhaps because the crystalloids in the tissue fluids are increased in concentration, but partly because a greater proportion of the water is influenced by its association with the body colloids. If it be assumed that water which remains unfrozen at −20° C. is 'bound' to the colloids, then it may be said that there is an increase in 'bound' water during hibernation. In winter-hardy species, this increase may take place without any change in the total water present [220].

It seems clear that the relation of water to the tissue colloids is one of the factors in cold hardiness; but there is so little agreement among colloid chemists on the subject of 'bound' and 'free' water that, at the present time, any generally acceptable explanation of the facts in terms of colloid chemistry is not possible. It has been suggested, also, that the binding of water to tissue colloids is one factor in the resistance of insects to desiccation [220].

The Temperature of Insects. We have seen that at high temperatures, insects above a certain size can keep themselves cool for short periods by evaporation of water from the body, or by making use of evaporating water in the environment [187]. At low temperatures, their bodies are often kept warmer than the surrounding air by the chemical changes going on within them. And both these methods of temperature control are used by the social Hymenoptera in maintaining the temperature of their nests or hives [126]. It seems that for the intense muscular activity of flight, a high body temperature is necessary; the large Sphingid moths are apparently unable to take flight immediately from rest; they first stand with the wings vibrating—shivering, as it were—until the temperature in the thorax has risen

above 30° C. Only then can they fly; and during flight the temperature will exceed 40° C.[72]. Similar changes occur in other insects during activity [260] but whether insects at rest will increase their metabolism in order to maintain the body temperature is at present uncertain.

Besides generating heat by muscular activity many insects make use of the sun's rays to warm their bodies to the optimum temperature [164, 260] their behaviour varying with the temperature attained; and it has often been suggested that the tendency of insects in cold climates to be dark in colour, is related to the absorption of radiant heat from the sun—though it is sometimes forgotten that this same dark colour will also favour the loss of heat during the night [222]. The range of external temperatures over which insects are normally active shows remarkable differences in different species, and does their resistance to high temperatures [260]. But the physiological basis of these differences is not known.

Respiratory Metabolism. The energy metabolism of insects varies, naturally, with the degree of muscular exertion. It therefore varies enormously in different species, and is much greater in the larva than in the pupa, and greater again in the adult [161] It depends also upon the temperature; but a rise in temperature not only increases the resting or 'basal' metabolism, but usually leads to greater activity. Only in very exceptional circumstances, therefore, is any simple mathematical relationship likely to be found between these two factors. Curves of various types, relating temperature with oxygen uptake, notably during pupal development, have been described mathematically by some authors; while others regard such curves as being really composed of a number of straight lines which intersect at 'critical points' where new metabolic processes are supposed to supervene [260].

The energy metabolism of such an insect as the bee, when at rest, is of the same order of magnitude as that of man: about 20 gm. calories per kilo. per minute. But during flight [145], this may be increased nearly 1,300 times, and the bee weighing 100 mg. may then burn sugar at the rate of 35 to 40 mg. per hour [158]—whereas in man, doing the maximum amount of work possible, the respiratory metabolism is increased only some 10 or 12 times. During activity, the respiratory quotient approximates to unity. During starvation, the quotient falls—indicating that, as in other animals, the stores of carbohydrate are consumed first, to be followed by protein and fat [57, 161].

Anaerobic Metabolism. Insects are remarkably resistant to lack of oxygen. Down to a low level of oxygen tension, the precise level varying in different insects, the oxygen uptake remains unchanged [114, 125]. Below this level it falls off; but many species can survive for long periods in the complete absence of air. The extra metabolism of activity very quickly ceases, and the insect becomes quiescent; the basal metabolism continues anaerobically. The type of chemical change does not alter: the unoxidized metabolites simply accumulate. Thus, by the time the insect is again restored to the air, it is greatly in arrears for oxygen; and in order to pay off this 'debt', and oxidize the lactic acid and other substances that have accumulated, its rate of oxygen consumption remains above the normal level for a long time (Fig. 11, B) [236]. During the anaerobic period, the blood naturally becomes more acid, the *p*H falling, in the case of the grasshopper, from 6·8 to 5·8, and the carbon dioxide capacity is reduced [29]; consequently, at very low tensions of oxygen, there may be a liberation of combined carbon dioxide [114]. This type of temporary anaerobic metabolism is a normal occurrence in the life of *Gastrophilus* (parasitic in the stomach of the horse) which can survive

as long as 17 days in the complete absence of oxygen [71]; experimentally, it occurs in insects of all kinds.

Now it has been repeatedly observed that during the pupal stage of insects, the rate of oxygen consumption first falls, and then rises again as the imaginal organs are formed; giving, altogether, a characteristic U-shaped curve [202]. The commonest explanation for this curve is that the intensity of

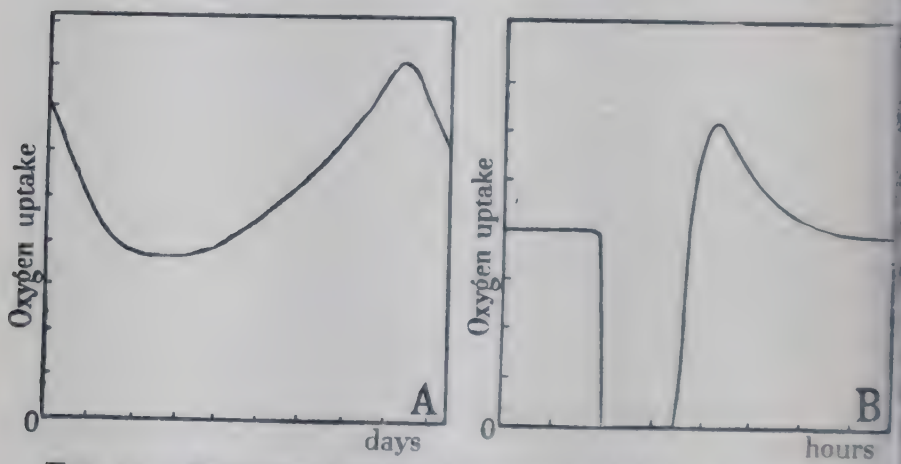

FIG. 11.—Ordinates: rate of oxygen uptake; abscissae: time

A, oxygen uptake during the whole pupal stage of 9½ days in *Galleria*, Lep. (after Taylor and Steinbach); B, oxygen uptake in grasshopper, *Melanoplus*. During the 75 minutes that the curve coincides with the base line, the insect was submerged in water (after Bodine).

metabolism is a measure of the amount of formed tissue present—the larval tissues in the early period, the adult tissues at the end. But another possible explanation, which does not seem to have been put forward, is that during the reconstruction of the tracheal system, metabolism becomes largely anaerobic, and the insect accumulates a temporary oxygen debt, of the same kind—though of course less in degree—as in the insect in nitrogen. There are three observations which support this notion: (i) during the pupal stage, the blood often becomes more acid and

the carbon dioxide capacity falls [22]; (ii) very low respiratory quotients are often observed, indicating an incomplete combustion of fats [179]; and (iii) a definite fall in oxygen uptake may be observed at the *end* of the pupal stage—suggesting that the oxygen debt has been paid off (Fig. 11, A) [249]. It is of interest to note that during both the pupal stage (in *Tenebrio* and other insects) [260] and the egg stage (in *Acilius*, Col.) [161], the total oxygen consumption during development is the same at all temperatures, although the *rate* of development varies enormously. Thus it would appear that the energy requirements of development are independent of the temperature.

Chemical Changes during Metamorphosis. The changes in the total composition of the insect body during metamorphosis naturally vary in different groups, with the different types of morphological change [202]. As a rule, the large stores of *glycogen* accumulated towards the end of larval life (these may exceed 33 per cent. of the dry weight of the body in the six-day-old bee larva [237]) fall steadily, almost reaching zero in the developed adult. The *fat* decreases rapidly at first, then more slowly (during the period of depressed oxygen consumption) and then rapidly again before emergence. Fat does not usually fall so low as glycogen, but only a small percentage of the original store persists in the adult. In the pupa of the Muscid *Lucilia*, it appears to be the unsaturated fatty acids which are consumed, the saturated acids remaining more or less unchanged [84]. The *protein* is sometimes largely used in the formation of the cocoon (the silkworm uses half its body protein for this purpose [202]); the remainder is extensively broken down during the early part of pupal life, the non-protein nitrogen, particularly the amino acids, increasing. With the growth of the new tissues, the process is reversed, and the amino acids fall [59] (p. 37). The inorganic phosphate follows the same course as the amino acids [59].

These changes, and the corresponding changes i other constituents and in the respiratory quotient represent, of course, only the summation of th processes of synthesis and breakdown that must b going on throughout metamorphosis. At times i must happen that these two processes will exactl balance in respect to a particular substance over given period, and then chemical analysis will revea no change at all. It is clear, therefore, that suc analyses of the whole animal are of rather limite interest; or rather, are impossible to interpret in telligently, until they have been correlated with th histological sequence of events. Conversely, intricat cytoplasmic changes are described in the fat bod and blood cells during metamorphosis, the chemica significance of which is almost completely unknown though it appears as though nuclear substance, fa and protein were being merged into a single materia easily transported to and assimilated by the growin imaginal tissues.[21]

Suspended Metabolism. From time to time certain of the metabolic activities of insects becom suspended for more or less prolonged periods. Thes periods of rest or, as it is termed, diapause, ma supervene at any stage: egg, larva, pupa or adult They are characterized by a reduction of activit in the motile stages, but more particularly by th cessation of growth—arrested development in th egg, larva and pupa, failure of the reproductive organ to mature in the adult. Therefore, although th respiratory metabolism is reduced during diapaus and, when it occurs in the pupal stage, the period o low oxygen uptake is enormously prolonged [118], dia pause is perhaps best regarded as a problem of growth.

In many insects this arrest may be brought abou by a variety of adverse conditions—cold, drought inadequate food and so forth—and normal growt is at once restored when conditions again becom normal[60]; or dormancy may be a direct effect o

temporary desiccation [52]. In other insects the arrest is *not* brought to an end in this way, and diapause continues until broken by some other stimulus, although the environmental conditions have again become favourable. And finally, there are many insects, in regions with a well-defined cold or dry season, which regularly spend the unfavourable months in a state of diapause ; in them, this state is assumed as the result of an inborn rhythm which manifests itself even when external conditions are uniformly favourable [60, 63].

Various hypotheses have been advanced to explain the occurrence of diapause : that it is an auto-intoxication from accumulated waste products [221], that it is the expression of an hereditary rhythm in the life cycle, and so forth. But the essential feature of diapause seems to be the cessation of growth. We shall see that growth is probably maintained by internal secretions (p. 93). The most probable hypothesis in regard to diapause is, therefore, that it is due to a failure in the hormones necessary for growth [287], induced in some cases by nutrition or by environmental conditions, in others by an inborn rhythm. The varied stimuli which will ' break ' the diapause : pricking, burning, severe cold [221], the oviposition or development of parasites [261], &c., may be pictured as evoking again the production of these hormones. An alternative hypothesis would picture diapause as due rather to a second factor which temporarily inhibits the normal growth process [30].

Pigment Metabolism. We have already seen that in the course of metabolism pigmented substances may arise as waste products (p. 59). Pigments may also be absorbed with the food and accumulate within the body : the flavone pigment in the wing-scales of the butterfly *Melanargia* [142], for example ; and the carotinoids in the blood of the potato beetle *Leptinotarsa*, and in the epidermal cells of the bug *Perillus* which preys upon it [150]. But it

is remarkable that apparently similar pigments in more or less related insects may be quite unrelated chemically: thus, the common red and orange pigments of many Hemiptera may be carotinoids from the food, anthocyanin-like or flavone-like pigments, perhaps also from the food [121, 150], or pigments of unknown nature formed in metabolism [286]; and the Pieridae may use their purine colours to mimic other butterflies the chemistry of whose pigments is quite different [130]. Similarly with the green pigments: in many cases these are synthesized by the insect itself, and have no relation to the chlorophyll of plants, even in phytophagous species; for their development is unaffected (in *Dixippus* [102], in locusts [86], and in many caterpillars [191]) by rearing them upon food containing no pigment; nor have they the chemical properties of chlorophyll and xanthophyll [86, 191]. The sexual differences in the blood of many caterpillars, which have been ascribed to differences in the utilization of plant pigments, are probably due rather to differences in the composition of the haemolymph proteins [191]. On the other hand, it is impossible to dogmatize on this subject; there are many who still believe that much of the green pigmentation of insects is due to altered chlorophyll [142, 262], and even that genetic differences in colour may result from differential absorption of the pigmented elements of which chlorophyll is composed [100].

The other type of insect pigment is the insoluble black substance melanin, which is formed in the presence of oxygen by the action of an oxidizing enzyme upon some colourless aromatic precursor, the 'chromogen'. Melanin-producing enzymes are generally diffused throughout the blood and tissues and secretions of insects, particularly near the time of pupation when much black pigment is often formed [70]; the chromogens are usually deposited in restricted areas, and so determine the colour patterns that develop [107].

The melanogenic enzymes can act upon a great variety of chromogens: tyrosine (monoxyphenylalanine), 'dopa' (dioxyphenylalanine) and various other polyphenols; and the enzyme concerned is termed tyrosinase, 'dopa'-oxidase, polyphenolase, according to the substrate used. But it is not certain whether in fact more than one enzyme is present, and in few cases has the natural chromogen been recognized. In the tissues and in the cocoons of certain Lepidoptera (*Samia cecropia*, *Eriogaster lanestris*, &c.[212]) and in the elytra of *Melolontha* [228], the spontaneously oxidizable 'dopa' has been demonstrated; and in the mealworm *Tenebrio*, dioxyphenylacetic acid has been proved to be one of the chromogens present [228]. But it is, of course, very probable that more than one chromogen may be concerned in a given insect; indeed, one view of the significance of melanin formation is that it provides an excretory mechanism for disposing of sundry toxic phenols arising in metabolism. Experimentally, the quantity of melanin formed can be widely varied by changes in the external conditions, notably the temperature [121, 150, 227]. In some cases (*Habrobracon*, Hym.), these effects may be transmitted to the offspring up to the second generation [144].

Melanin may be incorporated in the substance of the cuticle (pp. 2, 11), or deposited in granules in the epidermal cells. The other pigments may be in solution in the blood or in the fat droplets of the cells (lipochromes), or deposited as granules in the epidermis or other tissues, or between the layers of the wing scales.

In some insects the coloration may be strikingly influenced by external factors. Sometimes, notably in the stick insect *Dixippus*, such changes are reversible—the so-called 'physiological colour change'. There are no discrete chromatophores in these cases, there is simply a migration of pigment granules, a clumping or spreading, in all the epidermal cells [102].

In *Dixippus* this change may be brought about by a great variety of stimuli: temperature, narcotics, osmotic changes in the blood, mechanical pressure, all of which act directly upon the epidermal cells; and optical stimuli and humidity, which act through the eyes and tracheal system respectively, and then, by way of a centre in the brain, lead apparently to the secretion of a hormone into the blood, which determines the pigment movements [8, 102]. These pigment changes follow, also, a diurnal rhythm (the insect is dark by night and pale by day) which, though determined primarily by illumination, may persist for several weeks in complete darkness [102].

In these same insects, if the factors or stimuli already enumerated continue to act over long periods, the amounts of the different pigments formed may be permanently changed; and this may be effected, also, by nutrition, particularly by the moisture of the food. This permanent effect is termed 'morphological colour change'; but when brought about by optical stimuli, at any rate, it appears again to be produced, like the temporary change, by way of the nerve centre and the internal secretion [8]. The co-ordination of these mechanisms may lead to remarkable resemblances to their background in various Orthoptera [86].

As was shown by Poulton many years ago, larvae and pupae of certain Lepidoptera also possess wonderful powers of acquiring the tone or coloration of their background. This phenomenon has been analysed most carefully in the case of *Picris* pupae. In these the quantity of pigment deposited in the cuticle appears to be determined by the specific quality of the light received into the eyes of the pupating larva, acting through a centre situated in the head [35].

Another very striking colour change is that in locusts, the solitary phases of which are quite differently pigmented from the gregarious phases. The

gregarious type of coloration can be evoked by crowding the young forms together, and there is evidence that the factor responsible for the colour change is the incessant muscular activity which overcrowding causes. It has been suggested that the active muscles produce a substance (provisionally called 'locustine') responsible for this change [86]; but it is perhaps worth considering whether the factor in question may not be an increase in the acidity of the blood resulting from the ceaseless muscular contraction, acting perhaps directly, perhaps by way of the pigmentation centre.

CHAPTER VII

REPRODUCTION AND GROWTH

THE reproduction of insects forms one of the most remarkable chapters in their natural history. The structural adaptations for copulation, the control of the sperm in the body of the female, the micropylar arrangements in the egg, which allow fertilization through the fully formed shell, are remarkable enough. But the *curiosities* of insect reproduction: parthenogenesis, occurring sporadically, regularly or, in some species, apparently exclusively; viviparity, sometimes of newly hatched larvae, sometimes of single full grown larvae that have been nourished in the uterine cavity by special 'milk glands'; polyembryony in parasitic insects, in which a single egg may give rise to several hundreds of larvae; and paedogenesis, where the ova in the young ovaries of larvae or pupae ripen prematurely and develop into larvae which disrupt their parent host—all these phenomena present most fascinating problems [141]. Sometimes these abnormal paedogenetic or parthenogenetic generations may alternate with generations of the ordinary sexual type; and it is this alternation, due sometimes to inborn factors, sometimes, apparently, to environmental conditions, which make these matters specially interesting from a physiological point of view. But, at present, the physiological factors at work are quite obscure, and in this chapter we shall confine our attention to the more prosaic aspects of subsequent growth.

Growth. The phenomena of growth and develop-

ment in insects are, in broad outline, like those of higher animals. At one pole of the egg there is a centre (analogous, perhaps, with the organization centre of vertebrates) which determines differentiation in the embryonic germ [216, 231]; once differentiation has begun, development, co-ordinated by some unknown mechanism, proceeds until the insect hatches; then follows a period of growth, ending in maturity and reproduction. As in other animals, there is often a change in the proportions of the body as it increases in size; and when this is the case, the disproportion follows the law of disharmony or heterogony.* This law, the physiological significance of which is quite unknown, applies equally to morphological dimensions and to the concentration of chemical constituents [250].

But upon this general background are superimposed some special phenomena, conditioned by the make-up of the insect; and it is in these that we are mainly interested. In the first place, the cuticle is so constructed that once formed it cannot grow in surface area. If it is soft and much folded it may *stretch* gradually, and then the insect may increase continuously in length as it does in weight. This happens in the larvae of flies (e.g. *Drosophila*) and Lepidoptera (e.g. *Galleria*) [250]; but even in these insects there are hard regions of the cuticle which can grow only by replacement at the time of moulting. The growth of such parts is, therefore, discontinuous; and when the greater part of the insect is encased in a rigid cuticle, the growth in length of the whole body is likewise discontinuous, and takes place in a series of steps (*Sphodromantis* [214], *Dixippus* [80], *Gerris* [250]).

It was observed long ago by Dyar, working with the larvae of Lepidoptera, that the linear dimensions of the hard parts increased at each moult by a constant

* That is, that the logarithm of the dimension of the part is proportional to the logarithm of the dimension of the whole ($y = Kx^a$).

ratio, usually of the order of 1·4 (Dyar's law) [141]. More recently, it has been shown that various non-metabolic insects (*Sphodromantis* [214], *Dixippus* [80]) approximately double in weight from one moult to the next, while their linear dimensions increase 1·26 (i.e. $\sqrt[3]{2}$) times. This growth factor of 2 was first demonstrated by Przibram and Megušar [214]; it is perhaps best regarded simply as a special case of Dyar's law [250]; but it is sometimes referred to as 'Przibram's factor', and an attempt has been made, first by Przibram himself and later by others, to prove that this factor is universally applicable to insect growth [26]. This is only possible by introducing the conception of 'latent divisions' and supposing that the insect can multiply its weight by 2, perhaps several times, without moulting. In this way the growth of any insect can be made more or less to obey the same law. The physiological basis proposed by Przibram to explain his factor was that at each moult (or at each latent division) every cell in the insect body divides into two. But what histological evidence exists is definitely opposed to this improbable hypothesis. For in the Muscidae, almost the whole of larval growth is accomplished by increase in size of the cells without multiplication [208], and in hemimetabolic insects there is much cellular breakdown and reconstruction besides the irregularly distributed cell divisions [286].

We have seen that at the time of moulting, the insect enlarges its surface area by swallowing air or water (p. 13). In the latter case (*Aeschna* [232], *Notonecta* [250], &c.) the resulting curve for growth in weight is peculiar and shows an abrupt rise immediately after moulting, followed by a more or less level period during which the ingested water is gradually incorporated as true growth (Fig. 12, B). Equally curious is the growth curve of the blood-sucking bugs (*Cimex*, *Rhodnius*) which take only a single gigantic meal during each moulting stage, so that the weight

curve shows a series of acute peaks gradually rising to a higher level (Fig. 12, C) [51].

Moulting. The chief interest of insect growth centres round the phenomenon of moulting or ecdysis [148]. This is essentially a process of growth; for it is the only means by which the hard parts can

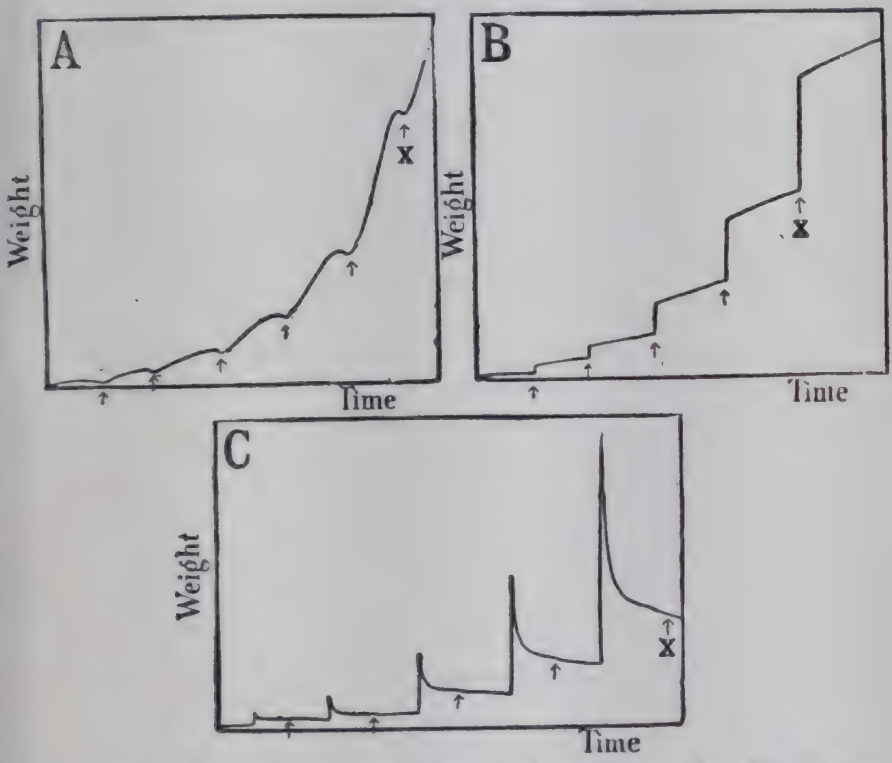

FIG. 12.—Growth curves; semischematic: A, *Dixippus*, (modified after Teissier); B, *Gerris*, Hem. (modified after Teissier); C, *Rhodnius*, Hem. (modified after Buxton)

The arrows indicate the time of moulting; the insect becomes adult at *x*.

increase in size (p. 12). There is no doubt, therefore, that growth is one factor that determines moulting. But in some insects (*Tineola* [256], *Tenebrio* [250]) moulting can occur repeatedly during starvation and without any enlargement: *Tineola* may sometimes develop a sort of 'moulting fever' and cast the skin as many as eight times in two or three days [256]; and adult

Collembola will continue to moult without change in size or organization [250]. There must therefore be some other factor at work. It is natural to suppose that this factor is of the nature of a hormone; and there is some experimental evidence of this, for if the blood of *normal* caterpillars is injected into other caterpillars near their time of moulting, the onset of moulting is delayed; but if the blood of *moulting* caterpillars is injected, moulting is not delayed. From which it is inferred that the process has actually been accelerated [48]. More convincing evidence is afforded by the fact that epidermal structures transplanted from one caterpillar to another of different age, even of a different species, undergo ecdysis at the same time as their new host [27]. And the presence of a moulting hormone has been clearly demonstrated in some recent experiments with the bug *Rhodnius prolixus* [287]. *Rhodnius* requires only a single feed in each of its five stages; moulting takes place at a definite interval after each meal. In the fifth or final nymph, this interval is about 28 days. Now, if the recently fed insects are decapitated before a certain 'critical period' (about 7 days after feeding), they fail to moult, although some of them may survive more than twelve months. If decapitated later than this, they will moult. But by allowing the blood from an insect decapitated 8 days after feeding to flow into an insect decapitated 1 day after feeding, the latter may be caused to moult.

The next question is the source of this hormone. One suggestion is that it comes from the 'moulting glands' (Verson's glands) in the epidermis [48, 139]; another, that it comes from the oenocytes [153]—both of which organs show a cycle of secretory activity which synchronizes with moulting [286]. But it has been shown that in *Rhodnius* neither of these hypotheses is tenable; because moulting begins before the moulting glands are differentiated and before the oenocytes reach the height of their activity [286]. Now

we have seen that decapitation inhibits moulting in *Rhodnius*; which suggests (though of course it does not prove) that the source of the hormone is in the head. Of the organs in the head, the only one which shows distinct changes during this period is the corpus allatum, the cells of which swell up to a maximum at about the seventh day after feeding, and then diminish. It seems likely, therefore (although the evidence is still very incomplete) that the corpora allata (which are nests of glandular cells budded off from the epidermis [201], like the endocrine organs of vertebrates, and innervated by the visceral nervous system) are the source of the moulting hormone [287].

As to the stimulus which causes secretion of this hormone: there is evidence that the stimulus to moulting in *Rhodnius* is the stretching of the abdomen by the meal; and section of the nerve cord in the prothorax inhibits moulting like decapitation. This suggests that moulting is started in *Rhodnius* by a nervous stimulus to the brain. But this cannot, of course, be a general explanation, applicable to those insects which moult repeatedly though starved.

Metamorphosis. Growth in holometabolic insects (Coleoptera, Lepidoptera, Hymenoptera, Diptera), that is, insects in which the adult is morphologically very unlike the young, and in which a resting pupal stage is interposed between the final larva and the imago, is generally pictured as a competition between larval and imaginal cells. Throughout larval life the former have the upper hand, and the imaginal cells, in the form of single 'histoblasts' or clusters of undifferentiated cells termed 'imaginal germs', are held in an embryonic state. Metamorphosis takes place when the larval cells die ('histolysis') and the imaginal cells escape from the influence that has restrained them, and proceed to grow and differentiate ('histogenesis'). That is, of course, a very crude conception of the process; for there is no absolute distinction between larval and

imaginal tissues. Even in the extreme case of the Diptera, many larval organs (Malpighian tubes; certain muscle groups) are remodelled without much change to form those of the adult [208]; and, conversely, a certain amount of histolysis takes place even during the ordinary larval moults [211, 286].

Thus, physiologically, metamorphosis differs from moulting only in degree: it is a moulting process, typically occupying two stages, in which the morphological changes are extreme. Now at the final moult of hemimetabolic insects (Hemiptera, Odonata, &c.) there is, again, a morphological transformation which is far more extreme than at the preceding moults. It is probably justifiable, therefore, to compare the physiology of this final moult of these 'exopterygote' insects with that of metamorphosis in the 'endopterygote' groups; and to suggest that the two types of development are likely to be controlled by similar factors.

Many hypotheses have been advanced to explain the initiation of metamorphosis: the intoxication of the larval tissues by accumulated waste products [141]; their asphyxiation by carbon dioxide [141], or their autolysis induced by other acids [22]; the failure of hypothetical secretions from the larval cells, which are supposed to have held the embryonic adult tissues quiescent, and kept the phagocytes at bay [208]; the overgrowth in size of the larval cells resulting in their death from starvation [254]; the awakening of the adult tissues by secretions from the genital glands [208], or by tyrosinase secreted into the blood [70].

The current conception is that metamorphosis, like moulting, is initiated by a hormone, and that this hormone differs in quality from that which causes moulting [27]. We have seen that decapitation of *Rhodnius* nymphs, before a certain critical period after feeding, prevents moulting; after this period normal moulting occurs. But if the fourth-, third-, second-, even the first-stage nymphs are decapitated

around the critical period, a certain number of them suffer a premature 'metamorphosis' and develop the characters of diminutive adults [287]. One must, therefore, conclude that the head exerts two influences: (i) it initiates moulting; (ii) it inhibits the realization of the imaginal characters until the insect is fully grown. And if one may generalize from a single hemimetabolic insect, and apply this interpretation to holometabolic insects, then the most probable mechanism of the control of metamorphosis is the inhibition of the imaginal germs, and of imaginal differentiation in general, by a hormone controlled by the brain. This hypothesis has already been put forward by Kopeć to explain metamorphosis in *Lymantria*, but upon very indirect evidence which he himself has later come to doubt [157]. On the other hand, Kopeć has produced good evidence that the brain (or some closely associated organ) is necessary for the initiation of the pupal moult [157].

This conception, of two competing hormones, one inducing growth, the other inhibiting metamorphosis, provides an explanation of 'prothetely'—the occasional appearance of pupal characters in mature larvae of certain beetles (*Tenebrio*, &c.[175]) and Lepidoptera (*Lymantria*, &c.[104])—if it be supposed that this phenomenon represents a partial escape of the embryonic tissues from the restraining influence of the inhibitory hormone. This condition finds a parallel in *Rhodnius*; for of those early nymphs decapitated around the 'critical period', while some show unmistakable adult characters, others show only some slight modifications towards the adult form [287].

Further, the condition of *Rhodnius* nymphs decapitated before the 'critical period', which slowly digest and metabolize their food, but fail to grow, is very suggestive of the state of diapause in normal insects (p. 80).

Histolysis and Histogenesis. There has been much controversy as to the mechanism of breakdown

of the larval tissues at metamorphosis. All that certain is that at a given stage the imaginal histobla first begin to proliferate rapidly, then each tiss that is to suffer histolysis disintegrates and d solves [211]. It is uncertain whether the cytoly agents come from the dying tissues themselves whether they are secreted into the blood by t leucocytes or other cells [208]. Sometimes the pha cytic cells in the blood invade and seem by their o activities to disrupt *apparently* healthy tissues [2 as a rule, obvious cytolysis is visible before the arriv phagocytes absorb and digest the products [205], som times the whole process of solution takes place witho the intervention of phagocytic cells [203, 237]; and oft all these types of breakdown occur in different pa of the same insect [254]. The final result is the sam the products of cytolysis of the larval cells serve nourish the growing tissues of the adult; though t intermediate stages of the process, which m obviously differ from one group of insects to anoth are not clearly known.

The co-ordination of all these processes to produ the adult form is the problem of orderly growth; wh is at present quite unsolved. The potentialities form seem generally to be inherent in the tiss themselves (wings, eyes, integument, &c.[159]) and be more or less independent of the other organs the body. Though the development of the musc in metamorphosis seems to depend upon their c nexion with the central nervous system [117].

Regeneration. The general obscurity of t factors controlling growth is well illustrated by t phenomena of regeneration. In the adult insect th are some slight powers of healing of wounds [178 w the formation of new cuticle, but no extensive pow of regeneration. In the pupa the same is true; the developing wings in the pupa of *Tenebrio* are c short, they round themselves off and approxim to the normal form, but there is no true regenera

tissue [182]. If the wing germs of Lepidoptera are ...ulated in the last larval stage, the damaged areas ... pattern are not made good; whereas if this is ...ne in the preceding instar, wings of normal proportions but reduced size regenerate; and if the germ is ...ided, reduplicated wings result [182]. At a still earlier ...ge, the wing germs can be extirpated completely ...d are formed anew from the hypodermis [182]. ...early, throughout development, as differentiation ...oceeds, there is a progressive loss of totipotence and ...generative power [213]; in the pupa everything is ...ally determined except for relatively slight changes ... colour pattern (p. 98) [87]. In hemimetabolic insects, ... the appendages are removed in the early larval ...ages, they show progressive regeneration at succeeding moults, and may attain almost normal proportions by the time the insect becomes adult. Here ...gain there is a progressive loss in regenerative power ... the insect grows older, which is due partly, but not ...ntirely, to the reduction in the number of moults ... the older insects, and the corresponding reduction ... the opportunities for growth [213].

In all these cases, the removal or partial removal ...f an organ results in more or less accelerated growth ...t the site of the wound. In the case of a limb, the ...ew growth is most rapid if removal is effected at the ...evel where autotomy (the spontaneous separation ...f an appendage) occurs naturally; but it is not ...ecessarily connected with the property of autotomy, ...or there is regeneration if appendages are cut through ...bove or below this level, and there is regeneration ...n appendages which cannot autotomize [245].

The influence which moulds the outward form of ...he new appendage seems to reside in the epidermis ...self: regeneration is unaffected by extirpation of ...he corresponding ganglion; though when this is done, ...either muscles nor nerves are formed within the ...ew appendage [156, 245]. In some cases, regeneration ... 'heteromorphous': in *Dixippus*, if the antenna

is cut through at the level of the flagellum, it regener ates as an antenna ; if it is amputated through on of the two basal segments it commonly regenerate as a leg, complete with tarsal claws [34]. But thoug this tendency exists, there is no absolute relatio between the level of section and the type of regenera tion [98].

Thus, the phenomena of regeneration, like those o normal growth, can be defined by certain laws—bu they are laws of growth and of regeneration ; the cannot yet be expressed in the simpler terms of phy siology, far less in terms of physics and chemistry

Determination of Sex. The genetic theory o sex determination has been admirably described b Dr. F. A. E. Crew in this series of monographs [6] This theory, which is based very largely on studie of insects, will explain the determination of sex bot in ordinary sexual reproduction and in parthenogenesis. It can probably be accepted that, in insects both primary and secondary sexual characters ar determined by the genetic make-up of the body cell —the secondary characters are not evoked by interna secretions from special glands, either in the gonad themselves or elsewhere. For (i), removal or trans plantation of the gonads at any stage of life is witho effect upon the secondary sexual characters [155] (ii) where the genetic constitution, in respect to sex of some body cells differs from that of others, a sexua mosaic or gynandromorph results, parts of which ar entirely male and other parts entirely female [61] ; an (iii) if the wing germs of Lepidoptera of one sex ar transplanted into the other sex, their sexual char acters are not influenced by their new environment [15

But in insects, as in other animals, the genetic se can be overridden by other factors, and it is thes other, physiological, factors in which we are inter ested here. The phenomena are most conveniently described in terms of Goldschmidt's well-known theor of intersexes [105]. Leaving aside the genetical analysis

this theory supposes that sex is determined by a quantitative balance between male determining and female determining factors within the nucleus of every cell. By analogy with the hormones of the animal body, these competing influences are often pictured as being *chemical* in nature (although, of course, they might be of some quite other kind)—that is, as hormones working inside the cell.

In the normal female the quantitative influence of the female determining factor outweighs that of the male; but the male factor is still there, and under certain circumstances its effect may become manifest. Thus, the balance between these factors, though normally determined according to the laws of genetics, may (according to those who accept this interpretation of the facts) be upset in several ways. (i) By crossing races in which the sex determining factors are of unmatched strength. Hence 'intersexes' result, the morphological characters of which are best explained by supposing that, owing to a difference in the rate at which the male and female factors come to exert their influence, the insect has developed up to a certain point as one sex and then 'switched over' to complete its development as the other [105]. (ii) By abnormal external temperatures, which are supposed again to upset the rate at which the two factors work, in such a way that the latent factor, which would normally be suppressed, is able to exert its specific effect, so that inter-sexual forms result [105]. (iii) By the action of internal parasites—notably the effect of *Stylops* upon certain Hymenoptera [223]. This effect was formerly called 'parasitic castration'; but it is more than the mere assumption of a *neuter* condition, it often involves a partial *reversal* of sex: females acquire male characteristics, and *vice versa*. In other words, the *latent* sex factor is again manifesting itself. This result seems to be due to starvation; for it occurs only in those Hymenoptera which receive a fixed ration to last the whole of larval life, and not

in those social forms which are fed according to their individual needs ; and the effects are exaggerated if more than one parasite is present [223]. In this connexion it is worth recalling that the sex ratio in certain Braconid parasites is influenced by the size of the host in which they mature [131]—perhaps this is a related phenomenon.

Determination of Other Characters. There is some indication that there may exist a parallel between the determination of other characters of bodily structure and those of sex. In other words, that Goldschmidt's theory may become a general theory of genetics [106]. For the most part, such body characters are determined genetically ; and when multinucleate eggs are fertilized by several spermatozoa carrying different genes, mosaics result in the adult insect, exactly comparable with the sexual mosaics or gynandromorphs [108]. But characters, ordinarily hereditable, can sometimes be elicited by changes in external conditions during development. These effects can be explained, as the occurrence of intersexes can be explained, by supposing that many morphological variations are induced by changes in the velocities of particular processes of development. Such changes in time relations may be brought about, on the one hand, by changes in the genes, or on the other, by alterations in the temperature or other factors, which influence one process more than another [103, 106].

The importance of rate of development in determining the final characters is well seen in certain butterflies with different spring and summer colour patterns : the summer form (*prorsa*) of *Araschnia levana* is modified into the spring form (*levana*) by exposure to cold during a brief susceptible period following pupation ; and the degree of modification is proportional to the length of time that elapses before emergence—the slower the individual development, the greater is the modification into *levana* [244].

It is interesting to note that the coloration centre in these cases (like the colour centre in *Dixippus*, &c. (p. 84)) is in the head : if the head is kept cold and the abdomen warm, cold forms result [103]. Disturbances in the velocities of different developmental processes may explain also the phenomenon of prothetely [104] (p. 93).

CHAPTER VIII

THE NERVOUS SYSTEM, SENSE ORGANS AND BEHAVIOUR

INSECTS are endowed with sensory or receptor organs of a high order, linked, through a complex nervous system, to an equally elaborate effector apparatus; and the complexity of behaviour that results from the co-operation of these systems has yet to be satisfactorily described in physiological terms. In the future, perhaps, the psychological method may provide an adequate description of insect behaviour; but most of the advances of the past thirty or forty years have been made along the lines of mechanistic physiology, and it will therefore be more helpful for our present purpose to approach the subject from that point of view.

The Nerve Cord. The central nervous system of insects generally shows a well-marked segmentation. Typically, each somite has its own pair of nerve centres or ganglia, giving off sensory and motor nerves and connected to the adjacent ganglia by a paired cord containing only nerve fibres. In virtue of these ganglia, each body segment enjoys a considerable degree of autonomy; probably each has its own respiratory centre controlling the movement of the corresponding spiracles, and each is capable of carrying out such reflex movements as do not involve the activity of other segments. The essential functions of these ganglia: the nature of the nervous discharge from the ganglion cells [2], the mechanism by which certain muscle groups are inhibited while their oppo-

nents contract [94], even the precise course of the reflex paths—are problems which have scarcely been studied in insects.

When a given reflex demands the co-operation of a number of body segments, there is situated in one of the ganglia a higher centre which co-ordinates the activities of the others. For example, the individual segments in the larva of *Corethra* are capable of contracting laterally upon stimulation, but true swimming movements are possible only if controlling centres in the third and fourth segments of the abdomen are intact [5]; in *Cloëon*, the respiratory movements of the gills can be effected by the segmental ganglia; but their normal rhythm is controlled by an inhibitory centre in the second thoracic ganglion and a stimulation centre in the sixth abdominal ganglion [5]; and so on for all the movements that have been studied [154]. In those insects in which most movements involve only the thorax, as in the winged forms, the ganglia have become enlarged and concentrated, and the isolated thorax is then capable of performing perfectly many of the motor functions—walking, clasping, vibration of the wings—of which the whole animal is capable [154].

The Brain. There is also a concentration of ganglia in the head: the suboesophageal ganglion and the supraoesophageal ganglion or 'brain'. Of these, the suboesophageal seems to be the equivalent of the motor ganglia that we have been discussing; it controls the movements of the mouth appendages [154], and may contain co-ordinating centres—as in caterpillars, where it controls the forward walking movements [154], and in the adult of *Aeschna*, where it inhibits the tenacious clasping reflex of the legs [12]. The brain, on the other hand, seems never to contain motor centres of this kind. It seems rather to be the central receptor for the abundant sense organs located in the head; and as such it orders the movements of the whole insect in accordance with the

stimuli which these receive. The reflex movements of the isolated body segments are themselves purposive in a limited degree; but when co-ordinated by the brain, all the body movements serve the purpose of the animal as a whole.

If the brain is removed, the reflex reactions of the body become exaggerated; it reacts to stimuli which in the normal insect would have no effect [17]; and movements, such as the cleaning movements in the bee, may continue without cessation for hours at a stretch [17]. Thus one function of the brain, one method by which it disciplines the organism, is to inhibit the too rigid execution of reflexes by the lower centres. If one half of the brain is destroyed, the insect tends to move in a circle towards the sound side. This reaction is due partly to the increased propulsive activity in the limbs on the operated side following the removal of inhibition [17]; partly to an effect of the brain in increasing the muscular tone of the flexor muscles on its own side [177]. But neither of these mechanisms will provide a complete explanation of the circus movement; for after mutilation of the limbs on either side, the performance of the muscles is so modified that the same movement still occurs [11]. The cause of this behaviour therefore lies deeper: each half of the brain, when acting alone, tends to bring about movement towards its own side —movement that requires the co-operation of muscles in all parts of the body [4, 12].

Reflex Responses in the Normal Insect. Comparatively simple reflexes undoubtedly play a large part in the responses of the normal insect; and our main problem is to describe the whole of insect behaviour in terms of such reflexes. Pressure upon the tarsus causes a reflex withdrawal of the leg; removal of the feet from contact with the ground evokes a turning over reflex [138] or initiates the vibration of the wings [90]; contamination of the antennae induces cleaning movements [138]. The mechanical

character of such reflexes is well seen in the cockroach: if the antenna is stimulated, and the insect is offered a bristle, it will clean the bristle and neglect the antenna [138]; and many insects will continue the cleaning movements after their antennae have been amputated. But though mechanical, these reflexes are purposive and plastic: the water beetle *Dytiscus*, deprived of one hind-leg will swim with the middle leg instead [18]; and if the fore-legs of the cockroach are removed, the stimulated antenna will be held by the middle pair [138].

Even the simplest of these reflexes involves many parts of the body, and some movements of the whole insect are also clearly reflex. This is notably the case with certain inhibitions. We have seen how loss of contact between the feet and the ground will initiate flight; conversely, flight is inhibited when contact is regained [90]. And contact with other parts of the body may similarly inhibit movement: the apparent preference for dark crevices in such insects as the moth *Amphipyra* [177], the earwig *Forficula* [271], and the bed-bug *Cimex*, depends in fact upon a reflex inhibition of their movements by contact ('thigmotaxis' or 'stereokinesis'). In the state of immobilization or 'akinesis' which such conditions induce, these insects may require strong stimuli to arouse them. Experimentally, a similar hypnotic state may be induced, in the earwig for example, by many kinds of constantly repeated stimulation [272]; and this state is doubtless related to the death-feigning reflex or 'thanatosis' shown by many insects when alarmed [23, 242].

Then insects moving at random may encounter unfavourable stimuli—too great heat or excessive cold for instance—whereupon they show a reflex 'avoiding reaction' and turn aside. By this mechanism, which is termed 'phobotaxis' [166], insects may be confined within a zone where the stimuli are optimal: houseflies, *Musca*, in a cold room with a

single bunsen burner will collect in a circle at a fixed distance around this source of heat [260].

Orientation. But neither in 'stereokinesis' nor in 'phobotaxis' is the insect truly orientated; it is either trapped in a given spot by reflex inhibition, or restricted to a given zone by 'avoiding reactions' [89]. Many insects, however, do show truly orientated movements ('topotaxis') in relation to such varied stimuli as light, sound, gravity, heat and odours [166]. Several mechanisms have been suggested by which these directed movements might be brought about. The simplest, known as 'tropotaxis', which is associated particularly with the name of Loeb, supposes that the tone of the muscles on either side of the insect's body is determined by the intensity of stimulus received in bilaterally symmetrical sense organs [177]. That being so, the insect is automatically turned by its muscles into such a position that stimulation on the two sides is equal; whereupon the muscular power becomes equal, and the insect moves in a straight line.

Many of the reactions of insects to light—both simple forms like the maggots of Muscids [177], and highly specialized animals like the adults of certain flies [99]—can be beautifully explained by this simple mechanism; and there can be little doubt that it does play a part in directing the movements of some insects. But it is certainly not the whole story. For although many insects, when offered two similar sources of light, will make for a point between them [170] (as was to be expected if they are directed by the tone of their muscles), and although many insects will move in circles if one eye is blackened over (as though the muscular tone on the two sides of the body were permanently unbalanced [177]), yet after a time, as the eye becomes adapted to the light, the higher forms at least will 'learn' to go in a straight line though they have but a single eye, or, with two eyes, they may select one of two sources of light and

go to that [258]. And after removal of one or more legs on either side, they will still make for the light in a straight line [184].

Such insects seem, in fact, to direct their movement to a chosen source of stimulus, to the neglect of others, as though they had the end in view. This type of orientation is therefore termed 'telotaxis' [166]. The response seems to be made up of a series of reflexes specifically related to the region of the eye that is stimulated [184] (like the fixation reflex in man); so that the insect finally turns until the image of the source of stimulus is received upon the region of clearest vision (in the insect with a single eye) or upon the corresponding points in the two retinae (in insects with both eyes intact) [184]. So exact has this reflex become in such insects as the fire-fly *Photinus*, that the single flash of light emitted by the female will cause the male to turn accurately in her direction [184].

This same 'fixation reflex' doubtless provides the basis of the response to moving objects that is shown by many insects. Some forms, like the larva of the dragon-fly [12], will follow any object moving near them; others, like the adult dragonfly, after turning momentarily to such an object, instantly leave it if it is not suitable for food [12], the initial reflex being inhibited by the higher centres. In the bug *Rhodnius*, the response to moving objects is normally elicited with difficulty, but it becomes very marked if the antennae are removed [289A].

Then there are insects which will move at a constant angle to a source of light; a method of orientation known as 'menotaxis' [166]. In some cases this response seems to result from the balanced turning effect of two lights—that from the source itself and that reflected from the background [55]. Sometimes included in this mechanism is the 'light-compass' orientation [50, 291] of ants and bees, which make use of the direction of the sun's rays in finding their way

back to the nest [89]. Certain aquatic insects (e.g *Notonecta*), maintain their position in running wate by a comparable mechanism—by keeping constan the image of objects on the bank. If these object are moved, the insect can be caused to move witl them [230]. Even such insects as Gyrinidae, whicl swim in all directions in the water surface, seem, sur prisingly enough, to maintain their position by th same mechanism [41].

It will be seen that the present tendency is t explain many of the reactions of insects to light a complex reflexes, and to restrict more and more th application of the muscle tonus hypothesis. Th same is true of the responses to warmth (in blooc sucking insects) and smell—stimuli which are per ceived mainly by the antennae. It is difficult t believe that such diffuse stimuli could cause accurat orientation by differential tonus effects on the tw sides of the body, that is, by 'tropotaxis' [177]. I has sometimes been suggested that odours are locate by 'phobotaxis' (although there is no evidence c any avoiding reaction to places where there is n smell) in combination with 'tropotaxis' [199, 267]. Bu the simplest mechanism is that which postulates reflex pursuit of the antennae into the region c optimal stimulation [289A]. This notion brings th response into line with the reflex response to ligh that is, with 'telotaxis'—though it is possible tha at short range, when the stimuli are very stron differential tonus effects may occur. As in the cas of light stimulation, there will be a tendency, as wa noted by Treviranus more than a hundred years ag for the insect with a single antenna to follow thi and so to turn in a circle when exposed to the attrac tive scent; and this tendency will naturally be mor marked when the antennae are relatively fixe structures not capable of individual movement [8 But none the less, the insect may be able to locat the source of smell very accurately although it ha

only one antenna [199, 267, 289A] which it could not do if its movements were controlled solely by tropotaxis.

Sense Organs: Mechanical Senses. We must now consider briefly the sense organs of insects from the point of view of their relation to these forms of orientation. The guiding sense of many insects is that of touch [271], subserved by articulated spines on the antennae and elsewhere. By administering suitable punishments and rewards, cockroaches can be trained, in a maze, to turn always to the right or the left; but when deprived of their chief organs of touch by removal of the antennae, this discrimination is lost [33]. The tactile sense is important also in stereokinesis (p. 103), though exactly what sense organs are concerned in this response is not established.

Another important source of orientation in insects, notably in the finding of food by many caterpillars [177], and by the earwig [271], is their movement against gravity (negative geotaxis). This reaction is not served by any special statocyst organ, but seems to depend upon receptors of tension in the muscles or tendons [14]—receptors which must also be of the greatest importance to the insect in maintaining its normal posture [14]. Closely related to, or perhaps identical with these organs are the tension receptors known as chordotonal organs. At their simplest (i) these serve to detect the external strains and pressures to which the body is subjected [123]; (ii) others are used to detect the strains at the base of the wings during flight; (iii) there is always a group at the apex of the pedicel of the antenna (Johnston's organ) which is probably stimulated by displacement of the antenna and so serves to detect air currents [77] or, sometimes, even air vibrations or sounds [77]; and, finally, (iv) they are developed in a highly specialized form, in association with a tympanic membrane, to provide the auditory organs present in many insects [77], by means of which the females of crickets

and other Orthoptera can recognize and locate t
specific sounds emitted by the males [10].

All these receptors, besides the specific effects wh
stimulation of them elicits, have the property
arousing the nervous system generally, and bringi
it into a reactive condition. They belong to the s
called 'stimulatory organs' [295] which serve both
maintain the muscle tone, and to enhance the kine
efficiency of the muscles when they are brought in
action. Prominent among the stimulatory orga
are the halteres of Diptera [47] and Strepsiptera [2
one important function of which is to sustain t
muscular vigour of the insect during flight by t
stimuli which their own vibration generates. In th
case the receptors seem to be partly the chordotor
organs but chiefly the abundant campaniform se
silla [257A].

Chemical Senses. The chemical senses of tas
and smell are developed in varying degree. Accep
ing the definition that what we perceive by the tong
are tastes and the flavours we detect by the nose a
odours [112], insects can recognize the tastes of sa
sweet, acid and bitter by means of receptors in th
mouth (*Apis* [97], &c.), on the antennae (Hymen
ptera) [169, 195], on the palpi (*Dytiscus* [225], *Geotrupes* [2
&c.) and on the tarsi (Diptera, Lepidoptera) [193
often in several of these sites in the same insec
They can detect odours chiefly by sensilla on th
antennae [96, 267], but to a lesser degree by the palps [2
While the 'general chemical sense', affected by pu
gent vapours, is present in many parts of the body [19
Receptors for the perception of specific flavours occu
in the pharynx of sucking insects, notably the H
miptera [268]; thus the blood-sucking bug *Rhodnius* w
rarely take up salt solution through a membran
unless a trace of haemoglobin is added to it [288].
. The sensitivity of the organs of taste in insec
may be very high: under conditions of starvatio
the butterfly *Pyrameis*, and the fly *Calliphora*, m

be able to detect with their tarsi concentrations of sugar of $\frac{1}{12,500}$ M or less [193]; the threshold for the human tongue lying between $\frac{1}{64}$—$\frac{1}{32}$ M. The apparent sweetness of the various sugars may be very different for insects and man [97]; and insects may differ in this respect not only between themselves, but even when the organs of taste on the tarsi are compared with those on the mouthparts: in *Calliphora*, lactose is apparently tasteless to the tarsi, but evokes a response from the mouthparts [194]. By a system of rewards and penalties, the water beetle *Dytiscus* may be trained to associate particular tastes with the presence of food [225].

Insects vary enormously in the extent to which their behaviour is directed by the sense of smell. Many species find their food largely by this means (cockroaches, crickets, *Drosophila*, &c. [289A]); butterflies often appear to be led to the food plant upon which to lay their eggs by some single odorous constituent in the leaves; parasitic Hymenoptera find by smell the larva in which to lay their eggs, sometimes detecting this from a distance, sometimes following the trail of scent which it has left behind it [199]; the following of trails of scent is doubtless very important also in the orientation of ants; but the highest development of this sense is seen in the males of those Lepidoptera (Lasiocampidae, &c.) which can detect and locate the female from distances of more than a mile by means of the olfactory organs in the antennae [89].

The potentialities of the sense of smell have been most fully studied in the case of the bee; and in this respect the bee's perceptions seem to be surprisingly like our own [96]. Flowers odourless to us are odourless to them; substances of unlike chemical composition which smell alike to us—such as nitrobenzol and oil of bitter almonds—are confused also by the bee; and the threshold concentration for odours to be detected seems to be of the same order

of magnitude for bee and man. Bees can readily be trained to associate the presence of a supply of food with particular scents; and they can retain the memory of such associations for several weeks—far longer than they can visual memories. But it is interesting to note that they can be trained only with aromatic odours such as might occur in flowers, and not to such substances as indol or asafoetida [96].

Vision. We have already seen how varied are the visual responses of insects. The receptor organs which serve these responses range from small groups of light-sensitive cells beneath lens-like thickenings of the cuticle, to the compound eyes of the highest forms, each with many thousands of retinal elements and capable of tolerably good image perception.

The stemmata, or simple eyes of larvae, which occur in the absence of compound eyes, are responsible for the orientating responses to light in maggots [81] and caterpillars [170]. In their highest development, which is attained in the predaceous larvae of Cicindelids and other beetles, they serve to locate the prey [92]; and although it is doubtful if they are capable of image perception, they can certainly perceive the movement of objects within the field of view. The ocelli, or simple eyes of adult insects, on the other hand, are optically unsuited to even the crudest type of image formation; for not only are the retinal elements few in number, but any image that is formed by the lens must fall far beyond the level of what elements exist [294]. In adult insects it is the compound eyes which are responsible for the movements to light: such movements do not occur if the compound eyes are covered, and only the ocelli remain [197].

What, then, is the function of the ocelli? So far, the only suggestion of the many that have been put forward [129], which has any experimental evidence to support it, is that they are stimulatory organs (p. 108) which accelerate phototaxis by in-

creasing the sensitivity of the brain to light-stimuli received through the compound eyes. Thus the response of *Drosophila* to light is appreciably more rapid and more persistent if the ocelli are intact than if they are blackened [31]. It must be realized that the light sense organs have two functions: a phototactic or orientating function, such as we have already discussed, and a photokinetic or stimulatory function (well seen in many day-flying butterflies which become quite incapable of flight in the absence of bright sunlight [295]). Now the phototactic response in *Drosophila* is essentially an escape reaction, manifested only when the insect is alarmed. The photokinetic ocelli increase its efficiency.

But whenever a faceted compound eye is present, no matter how few may be the retinal elements it contains, these will inevitably receive different intensities of light from different parts of the visual field; and some kind of visual pattern must always result. Consequently, any movement in the visual field will at once be perceived by the changes in pattern it will produce. We have seen that many insects will turn towards an object that is moving; will turn, that is, until corresponding points of the two retinae are stimulated by it. Now the closer the object is to the insect, the nearer to the mid-line will be these corresponding points. Consequently, the insect may enjoy some of the advantages of binocular vision, and be able to judge accurately the distance of objects, even though its perception of images be rudimentary [92]; and like the larva of *Aeschna* [13] or the bug *Rhodnius* [289A] (when deprived of its antennae), it may attack with precision any object that moves within range.

In forms like the adult dragon-fly and the bee, image perception reaches a higher plane, and specific objects can be recognized; so that Sphingid moths, for instance, will endeavour to extract nectar from the flowers of wallpapers or from models of flowers [151].

By calculation and by experiment it has been estimated that the visual acuity of the bee, in the vertical axis, is about one-fiftieth that of man (in the horizontal axis the acuity is only about one-third of this, because the eye is more curved and each ommatidium has to cover a wider field—the bee, in fact, is astigmatic [15, 116]). But this degree of acuity is obtained only under optimal conditions of illumination. With poor illumination, both the visual acuity and the discrimination of different light intensities [293] are so greatly inferior to that of man, that the resolving power of the eye must be extremely feeble. None the less, these insects can recognize different forms, and can learn to associate with these the presence of food [95, 297]. The bee and other Hymenoptera can find their way over miles of country by means of landmarks [292], and can recognize the entrance to their own hive or nest by visual memory [204, 255].

Colour Vision. The visual perceptions, notably in flower-visiting insects, are greatly enhanced if the objects are coloured; insects possess, in fact, a well-developed colour vision [82, 95]. The histological basis of this colour vision is not certainly known, though it seems that each retinal element or ommatidium receives a double innervation (comparable with the rods and cones of vertebrates), one to perceive light and the other to perceive colour [113]. The functional significance of colours in the vision of insects is much better understood. Certain responses, such as the fixation reflex, are influenced only by the *luminosity* of the source of stimulus and not by its colour [226]. Such responses, therefore, afford a method of testing the subjective luminosity of different colours for different insects; and it has been shown that for many insects (*Mantis*, *Coccinella*, *Apis*) the luminosity of the visible spectrum is the same as for man with the eye dark adapted; for others (*Pieris*) it corresponds with the light adapted human eye [226]. Many insects can vary the amount of light entering the eye,

by movements of the pigment in the iris cells [206]; but whether this change has any influence on colour vision is not known.

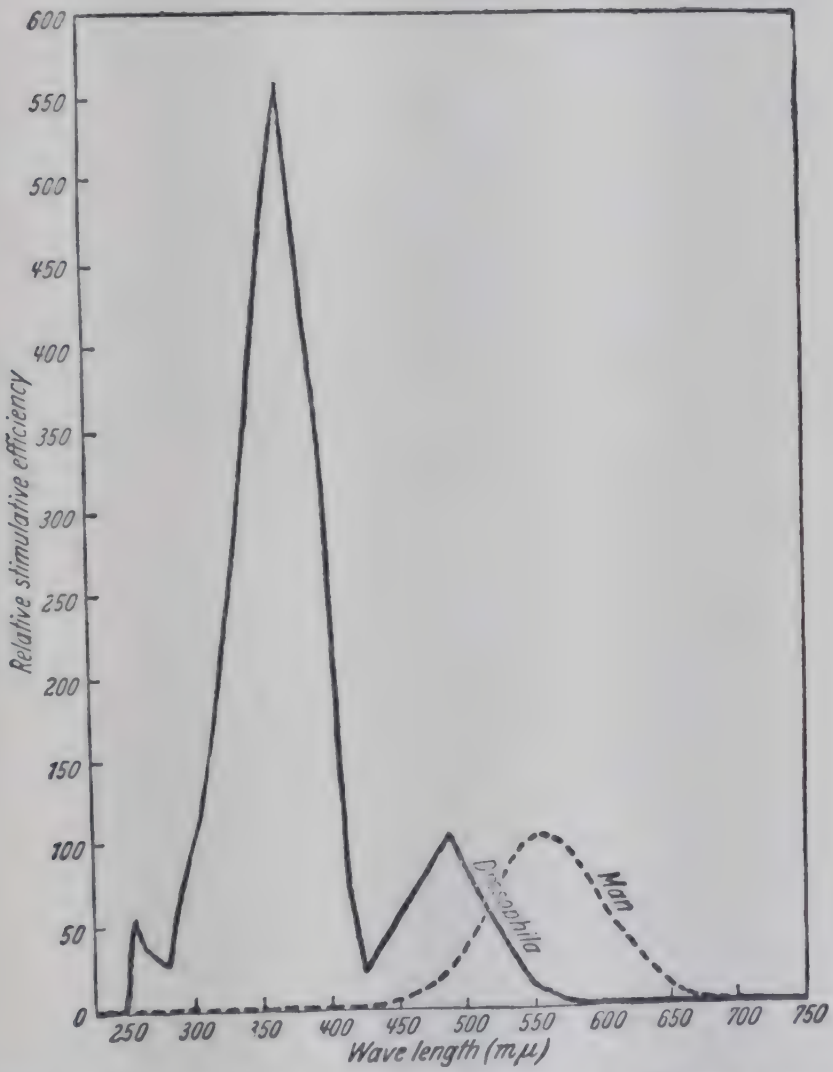

FIG. 13.—Relative stimulative efficiency of different wave lengths for man and *Drosophila*. (After Bertholf.)

Corresponding with these differences in apparent luminosity, there are differences in the visibility of the spectrum. Certain insects (*Apis* [95]; *Macroglossa*,

Lep.) are practically blind to red, but can see far into the ultra-violet [167]. Such insects may be attracted by the ultra-violet light reflected from certain flowers [178]; and they will cluster round screens illuminated with ultra-violet rays which are invisible to us [142]. Indeed, the stimulating efficiency of the ultra-violet part of the spectrum, for the honey-bee and for *Drosophila*, may be far greater than that of the regions visible to man (Fig. 13) [16, 224]; and although this effect may be due in some degree to the fluorescence of parts of the eye under ultra-violet illumination, this cannot account entirely for the phenomenon [189]. There must be a true perception of ultra-violet; and it is interesting to note that the limit of this perception is, approximately, the lower limit of the solar spectrum [16]. Other insects are capable of seeing red (Pieridae) [140], and associated with this is the shift in the apparent luminosity of colours that we have already noted.

Insects, like man, experience the phenomenon of simultaneous contrast; a grey field surrounded by yellow appears blue to the bee, a grey field surrounded by blue appears yellow [167].

Insect Behaviour. Most of the information on colour vision in insects, and a great deal of the more reliable information upon other senses, has been obtained by training experiments: stimuli which the insect can learn to associate with the presence of food, or with the location of its nest, are judged to be perceptible. Such experiments, of course, need the greatest care in their interpretation; for the insect may be guided by some other stimulus that has been overlooked by the experimenter; indeed, in the course of a single experiment, it may cease to be orientated by one stimulus and come to depend upon another [292]; and there are many who hold that the whole perceptual experience of the organism is integrated, as it were, into a pattern, and that it responds to general changes in this pattern, and *not*

to the isolated stimuli of which it is composed (Gestalt theory) [93, 124].

Thus, when we consider the behaviour of insects under natural conditions, we find them gaining their ends by an infinite variety of sensory impressions. Inborn reflexes, and reflexes 'conditioned' by the experience of the individual, certainly occur; but these are masked by inhibitions, and integrated by higher centres, in such a way that they serve constantly the needs and purposes of the insect as a whole. It is this unifying quality, that welds the organism together, and makes the whole something greater than the sum of the parts, which in the sphere of behaviour as in the sphere of growth still eludes physiological analysis.

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